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Methane Production in Native Ruminants

By

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled METHANE PRODUCTION IN NATIVE RUMINANTS submitted by JAYSON KENT GALBRAITH in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in ANIMAL SCIENCE.

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Date August 13, 1997

DEDICATION

To my parents:

Kathleen Sara and

John Lynn Galbraith (June 27, 1940 - January 13, 1997)

Who both helped, encouraged, put up with, and constantly motivated me.

ABSTRACT

Five female yearling bison (*Bison bison*) and wapiti (*Cervus elaphus*), and eight female yearling white-tailed deer (*Odocoileus virgianus*) were used in measurements of methane and heat production during March and May 1995. The digestibility of a sun-cured alfalfa pellet diet was also determined with each species. Feed digestibility was not affected ($p<0.05$) by animal species or period. Voluntary metabolizable energy intake during calorimetry measurements averaged over both periods was 514, 691, and 783 kJ $kg^{-0.75}$ for bison, wapiti, and white-tailed deer respectively. Methane production expressed as a percentage of gross energy intake was 6.6%, 5.2%, and 3.3% for bison, wapiti, and white-tailed deer respectively ($p<0.05$) and was higher ($p<0.05$) in May than in March. No differences could be detected in the maintenance energy requirements (kJ $kg^{-0.75}$) of the three species.

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Table of Contents

CHAPTER 1 INTRODUCTION 1

1.1 LITERATURE CITED 4

CHAPTER 2 LITERATURE REVIEW 5

2.1 THE GREENHOUSE EFFECT 5

2.2 GREENHOUSE GASES 5

2.3 METHANE 7
2.3.1 Effect of methane in the atmosphere 7
2.3.2 Sources of methane in the atmosphere 8
2.3.3 Ruminants' contribution to the global methane budget 9
2.3.4 Contribution of ruminants other than cattle to the greenhouse effect 10
2.3.5 Accuracy of global methane emission estimation 10

2.4 METHANE SINKS 11

2.5 FACTORS INFLUENCING METHANE PRODUCTION IN THE RUMINANT 12
2.5.1 Methanogenic bacteria 13

2.6 STRATEGIES TO REDUCE RUMEN METHANE PRODUCTION 15
2.6.1 Ionophores 16
2.6.2 Other chemical compounds 16
2.6.3 Defaunation 17
2.6.4 Lipids 18

2.7 METHODS FOR DETERMINING METHANE PRODUCTION 18

2.8 ENERGY 20
2.8.1 Units 20
2.8.2 Partitioning of Energy 20

2.9 METABOLIC RATE AND HEAT PRODUCTION 22
2.9.1 Seasonal maintenance requirements estimated from feeding trials and indirect calorimetry 23

2.10 DIGESTIVE PHYSIOLOGY OF WILD RUMINANTS 25
2.10.1 Digestive strategies 26
2.10.2 Digestibility of diets by different ruminants 29
2.10.3 Mean retention time 30

2.11 LITERATURE CITED 32

CHAPTER 3 METHANE PRODUCTION IN NATIVE RUMINANTS 42

3.1 INTRODUCTION 42

3.2 METHODS 44
3.2.1 Study area, animals, and diet 44
3.2.2 Digestibility trials 45
3.2.3 Methane production and oxygen utilization 46
3.2.4 Laboratory analysis 48
3.2.5 Statistical Analysis 49
3.3 RESULTS 50
3.3.1 Feed 50
3.3.2 Environmental temperature 50
3.3.3 General health of the animals 50
3.3.4 Handling considerations 51
3.3.5 Ad libitum intakes 52
3.3.6 Digestibility and Urinary Output 52
3.3.7 Methane production 53
3.3.8 DE and ME content of diet 53
3.3.9 Digestible and metabolizable energy intakes 54
3.3.10 Heat production and estimated maintenance requirements 54

3.4 DISCUSSION 59
3.4.1 Ad libitum intakes 59
3.4.2 Digestibility and urinary output 61
3.4.3 Methane Production 64
3.4.4 Metabolizable energy intake 68
3.4.5 Heat production and estimated maintenance requirements 69
3.4.6 DE and ME content of diet 73
3.4.7 Conclusions 73

3.5 LITERATURE CITED 75

CHAPTER 4 GENERAL DISCUSSION AND CONCLUSIONS 80

4.1 ACCEPTANCE OF THE DIET 80

4.2 LIMITATIONS OF THIS EXPERIMENT 80

4.3 FUTURE RESEARCH 82

4.4 IMPLICATIONS 83

4.5 LITERATURE CITED 85

CHAPTER 5 APPENDICES- RAW DATA 86

List of Tables

TABLE 2.1. GREENHOUSE GASSES, THEIR LIFETIME IN THE ATMOSPHERE, AND THEIR GLOBAL WARMING POTENTIAL.....7

TABLE 2.2. CURRENT ESTIMATES OF METHANE SOURCES IN THE ATMOSPHERE (TG^1/YEAR). 9

TABLE 2.3. COMPARATIVE DAILY FASTING METABOLIC RATES (KJ $KG^{-0.75}$ D^{-1}) FOR WINTER AND SUMMER AND THEIR CORRESPONDING CALCULATED ME_M (KJ $KG^{-0.75}$ D^{-1}). 23

TABLE 2.4. METABOLIZABLE ENERGY REQUIREMENTS FOR MAINTENANCE (ME_M) FOR WHITE-TAILED DEER AND WAPITI CALCULATED THROUGH INDIRECT CALORIMETRY (IC) OR FEEDING TRIALS (FT). 25

TABLE 2.5. DRY MATTER DIGESTIBILITIES OF RUMINANTS.....30

TABLE 2.6 MEAN RETENTION TIMES (MRT) OF DIGESTA IN THE DIGESTIVE TRACT OF VARIOUS RUMINANTS 30

TABLE 3.1 BODY WEIGHT AND AD LIBITUM INTAKES OF ALFALFA PELLET DRY MATTER (DMI) AT DIFFERENT TIMES IN THE EXPERIMENT. 55

TABLE 3.2. LEAST SQUARES MEANS OF DIGESTIBILITY, AND NITROGEN BALANCE IN BISON, WAPITI, AND DEER FED SUN-CURED ALFALFA PELLETS 56

TABLE 3.3. LEAST SQUARES MEANS OF METHANE PRODUCTION, HEAT PRODUCTION, AND CALCULATED METABOLIZABLE ENERGY REQUIREMENTS FOR MAINTENANCE (ME_M) IN BISON, WAPITI, AND WHITE-TAILED DEER.....57

TABLE 3.4 MEAN DIGESTIBLE ENERGY (DE) AND METABOLIZABLE ENERGY (ME) CONTENT OF DIET, AND ME:DE RATIOS FOR BISON , WAPITI, AND WHITE-TAILED DEER AT *AD LIBITUM* INTAKE DURING DIGESTIBILITY TRIAL.....58

List of Figures

FIGURE 2.1 CONTRIBUTION OF GASES TO THE GREENHOUSE EFFECT.....6

FIGURE 2.2 STEPS IN THE RUMEN LEADING TO THE FORMATION OF METHANE. 15

FIGURE 2.3 PARTITIONING OF ENERGY IN AN ANIMAL. 20

List of Abbreviations

ad lib- ad libitum
ADF- acid detergent fiber
d- day
DE- digestible energy
DM- dry matter
DMI- dry matter intake
GE- gross energy
GEI- gross energy intake
HP- heat production
J- joule
kg- kilogram
LCFA- long chain fatty acids
ME- metabolizable energy
ME_g- metabolizable energy required for gain
MEI- metabolizable energy intake
ME_m- metabolizable energy required for maintenance
MJ- mega joule
NDF- neutral detergent fiber
ppm- parts per million
Tg- terragram ($1x\ 10^9$ kg)
Yr- year

1. Introduction

Game ranching has been defined as the sustained commercial use of wild populations of hoofed mammals for production of meat and possibly sport-hunting opportunities (Stelfox 1993). Other reasons for farming wild animals are antlers and other by-products, raising brood stock, and protection of species (Teer 1993). Three common indigenous species on game farms in Canada are white-tailed deer (*Odocoileus virginianus*), wapiti (*Cervus elaphus*), and bison (*Bison bison*). Animal populations on game farms in Canada have increased to numbers of around 19144 wapiti, and 7039 white-tailed deer at the end of 1995 (Houdepohl 1997). Numbers of farmed bison are more difficult to determine since there is no mandatory registry as there is for white-tailed deer and wapiti. However, it was estimated that in 1996 there were around 28000 bison in Alberta, with Alberta's bison making up approximately 50% of the farmed population in Canada (Houdepohl 1997). As farmed indigenous species continue to increase in numbers additional research into digestion, and efficiency of feed utilization, such as outlined in this thesis, will be necessary to ensure maximal efficiency of production of the animals.

The greenhouse effect is a term referring to the buildup of gases in the atmosphere which causes a greenhouse-like effect in that heat is trapped within the earth's atmosphere and not allowed to escape into space. This causes an increase in global temperatures and has led many people to fear massive implications from resulting floods, erratic weather patterns, and melting glaciers. Over the next 50 years

it is expected that the global temperature will rise between 1.5 and 4.5°C (Environment Canada 1988).

Carbon dioxide is the single greatest contributor to the greenhouse effect and levels are rising at a rapid rate. Carbon dioxide concentrations are presently rising at an estimated 5% per year and have already increased by about 25% over the past 200 years (Environment Canada 1991).

Methane is the second largest contributor to the greenhouse effect. It too has been increasing and was at an estimated atmospheric concentration of 1.7 parts per million by volume (ppm) in 1989 compared to the pre-industrial revolution concentration of 0.7 ppm (Tyler 1991). Rice paddies and biomass burning are two sources of contemporary methane release into the atmosphere. Methane can be produced by anaerobic microbes in such places as ocean and lake beds, soils, and in the rumen of ruminant animals. The amount of methane released by cattle and other domestic ruminants has been studied and can be estimated with reasonable accuracy within North America. However, there is essentially no information on methane emissions from wild ruminants. With the rise of game farming, and the increasing concern with the greenhouse effect, a more accurate value for the emission of methane from wild ruminants on farms and in the wild is important. Also, it is important to know if domestic animals on farms produce more than the wild species they replaced.

The objectives of the research outlined in this thesis were to measure and compare methane emission from three wild ruminants, bison, wapiti, and white-tailed deer to test the hypotheses that the proportion of feed energy lost as methane differs

between species and that methane and heat production in these animals is seasonal. Using Hofmann's (1989) classification scheme of wild ungulates, it would be expected that bison, as a grazer, would lose proportionately more methane than either wapiti or deer which are intermediate feeders and concentrate selectors respectively. Concentrate selectors (deer) would be expected to lose proportionately the least methane among the three groups since their digestive system is geared towards an easily fermentable diet which passes through the digestive tract quicker than the diet of a grass/roughage eater.

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2. Literature Review

2.1 The greenhouse effect

The "greenhouse effect" is a phenomenon where gasses accumulate in the earth's atmosphere, trapping heat inside it. Short wave radiation travels through the atmosphere and is absorbed by the earth, and reradiated as and long wave radiation which is trapped inside the atmosphere. This results in heat being re-radiated back to the earth's surface causing an increase in both atmospheric and surface temperatures of the earth. The result of the greenhouse effect has been and will be, global warming. It is expected that by the year 2025, the average global temperature will rise by 1°C (Environment Canada 1991), and in the next 50 years the rise will be between 1.5 and 4.5°C (Environment Canada 1988). This would have profound impacts on agriculture, rainfall patterns, and borders of various ecosystems particularly in Canada where there are temperature extremes. A one meter rise of the level of the ocean is anticipated by the year 2050 (Environment Canada 1988) mostly due to melting glacial ice in the poles of the earth. This would cause severe flooding in low areas, and a decrease in the thickness and amount of ice at the poles.

2.2 Greenhouse gases

The main greenhouse gases in order of importance are: carbon dioxide (CO_2), methane (CH_4), chlorofluorocarbons (CFC's), and nitrous oxide (N_2O). The current percentage contribution of these gasses to the greenhouse effect is given in Fig. 2.1.

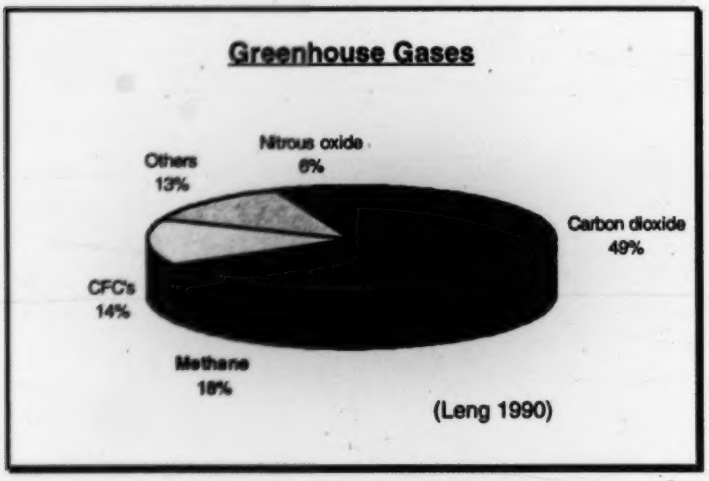

FIG. 2.1 CONTRIBUTION OF GASES TO THE GREENHOUSE EFFECT.

Greenhouse gases are needed, at certain levels, to maintain earth's temperature at an average temperature of around 15°C (Tyler 1991). Without them the earth's average temperature would be about -18°C (Schneider 1989). It is now well known that human activities have increased the concentrations of naturally occurring greenhouse gases. Atmospheric concentrations of carbon dioxide have increased from about 280 ppm (Barnola et al. 1987) some 200 years ago, to 350 ppm in the year 1989 (Keeling et al. 1989). The growth in CO_2 concentrations began at the same time that the industrial revolution began, and can almost certainly be attributed to anthropogenic activities. In 1989, methane was at a level of 1.7 ppm whereas before the industrial revolution it was at 0.7 ppm (Tyler 1991). It has been estimated that atmospheric methane is increasing at rates ranging from 0.6% per year (Steele et al. 1992), to 1.0% per year (Moss 1993; Thompson et al. 1992) due to increased anthropogenic activities such as biomass burning and rice paddy production.

The comparison of gasses to the action of CO_2 is called the global warming potential. The value for the global warming potential varies depending on efficiency for trapping solar radiation and the time line chosen for the comparison, because gasses have different ranges of electromagnetic absorption and varied lifetimes in the air. Table 2.1 lists the major greenhouse gasses with their lifetime and their global warming potential. Since methane does have such a short decay time in the atmosphere, it is a good candidate for control. Emissions would only need to be reduced by 10% to stop the yearly increase in atmospheric concentration (U.S. EPA 1993d).

Table 2.1. Greenhouse gasses, their lifetime in the atmosphere, and their global warming potential.

Greenhouse Gas	Lifetime in the atmosphere	Global warming potential (multiple of CO_2)
CO_2	variable ~ 100yrs	1
CH_4	12yrs	21
N_2O	120yrs	310
CFC	50-1700	3800-9100

(IPCC 1995)

2.3 Methane

2.3.1 Effect of methane in the atmosphere

Methane is a colorless, odorless hydrocarbon with a critical temperature of -82.2 °C (Chynoweth 1996). Methane is a strong absorber in the infrared portion of the electromagnetic spectrum with strong absorption centered in the 7.7 μm spectrum, a range in which other atmospheric gases do not strongly absorb (Tyler 1991). Methane not only absorbs energy in the infrared spectrum directly, but also reacts

photochemically to produce other greenhouse gases such as ozone and CO_2 (Chynoweth 1996).

As seen in Fig. 2.1, methane contributes about 18% to the total greenhouse effect (Leng 1990). Its significance is influenced by the fact that the direct effect of methane is 21-fold greater than CO_2 (for a 100 year period) on a weight basis, with the decay time for methane being 10 years compared to 120 years for CO_2 (Rohde 1990). Put another way, it has been calculated that 1 kg of methane has 63 times the warming effect of 1 kg of carbon dioxide for 20 years after emission (Houghton et al. 1992).

2.3.2 Sources of methane in the atmosphere

Methane is an end product of several chemical reactions which take place in anaerobic environments such as ocean and lake sediments, and animal digestive tracts. It is in these environments that electron acceptors such as dioxygen, nitrate, and sulfate are depleted and replaced by carbon dioxide as an electron acceptor which results in the production of methane (Chynoweth and Isaacson 1987). The principal substrates of methanogenesis are acetate, hydrogen, and carbon dioxide (or formate).

From Table 2.2, the average estimated amount of methane emitted into the atmosphere from various sources are as follows; enteric fermentation in ruminant animals is 80 Tg with values ranging from 65- 120 Tg, 85 Tg from paddy rice production, and 50 Tg from biomass burning. However, many of the estimates include a large range of numbers. For example, the paddy rice figure of 60 Tg/yr (Watson, 1992) is much lower than the estimate by Fung (1990) of 100 Tg/yr. These estimates are open to question and probably change considerably from year to year.

Table 2.2. Current estimates of methane sources in the atmosphere (Tg^1/year).

Source	Khalil and Rasmussen 1987	Bingmer and Crutzen 1987	Cicerone and Oremland 1988	IPCC 1990	Fung 1990	Watson et al. 1992	Mean
Ruminant	120	70-80	65-100	65-100	80	80	87
Paddy fields	95	18-91	60-170	-	100	60	85
Biomass burning	25	30-100	50-100	20-80	45	40	50
Land fills	-	30-70	30-70	20-70	40	30	43
Coal mining	-	35	25-45	-	35	100	51
Gas leaks and vents	40	0-35	25-55	40-100	40	-	42
Other anthropogenic	40	-	-	-	-	50	45
Swamps & marshes	150	26-137	100-200	100-200	80	115	121
Lakes and oceans	23	-	6-45	6-45	10	15	20
Tundra	12	-	-	-	35	-	24
Other natural	48	0-30	10-100	-	25	25	34
Total anthropogenic	320	183-411	255-535	145-350	350	360	328
Total natural	233	26-167	116-345	116-445	150	155	191
Total	553	209-578	371-880	261-795	500	515	602

(Adapted from Bandyopadhyay et al. 1996)

[1] $1Tg = 1 \times 10^9$ Kg

2.3.3 Ruminants' contribution to the global methane budget

Ruminant animals have multi-chambered stomachs which utilize microbes to aid in the digestion of cellulose and other cell wall portions of plant diets. The range of methane emissions from ruminants into the atmosphere ranges from 65 - 120 Tg/ year (Table 2.2). Of the animal methane emissions, approximately 73% is derived from the world's cattle population (Johnson and Johnson 1995). The remainder comes from other ruminant animals such as sheep, goats, camels, bison, deer, and wapiti or monogastric animals. The contribution of monogastric animals to the total global

methane emission has been estimated at only 3-4% (~2.9Tg) of the total animal release of methane (Crutzen et al. 1986).

2.3.4 Contribution of ruminants other than cattle to the greenhouse effect

Using the value from Leng (1990) of 18% for the overall contribution of methane to the greenhouse effect, and assuming: a total methane release of 602 Tg/yr (Table 2.2) an average value of 87 Tg (Table 2.2) for the estimated methane produced by ruminants, and that 73% of the animal methane contribution is from cattle alone (Johnson and Johnson 1995), then the contribution of "other" animals to the greenhouse effect can be estimated. When this is done the contribution of the greenhouse effect which comes from animals other than cattle such as sheep, goats, bison, wapiti, deer, and camels is 3.9% of the total global methane emission and 0.7% of the total greenhouse effect.

2.3.5 Accuracy of global methane emission estimation

Most global estimates of methane emissions from ruminants are based on mean emission factors multiplied by the approximated number of animals in a variety of ruminant groups (Johnson et al. 1994). This is done by using an estimated percentage of feed gross energy loss to methane, multiplying this number by the estimated annual gross energy intake, and then converting the energy value (MJ) to a mass such as kg or Tg (EPA 1989). A problem with generalizing groups of ruminants, by using formulas to calculate methane emissions, is the significantly different metabolic and digestive properties between and within species. For example, in North America where cattle in feedlots are frequently fed very high grain diets of over 90%, the commonly used value of 6% of gross energy intake (GEI) lost as methane would

be a huge overestimate as the measured values for cattle under these conditions frequently fall between 2 and 3 % of feed GEI (Abo-Omar 1989; Carmean 1991; Hutcheson 1994). In contrast, Sika deer (*Cervus nippon*) lose 6.6% of their GEI to methane (on an undisclosed diet) as expressed by the equation CH4 (kJ/d) = 0.07GEI (kJ/d) - 101.04 (r^2=0.9) (Zhonokuan et al. 1996). This shows the great variation in the amount of methane lost by different species with different feed types.

2.4 Methane Sinks

Microorganisms can remove methane through both aerobic (Rudd and Taylor 1980) and anaerobic oxidation (Alperin and Reeburgh 1984). It has been shown that methane is oxidized in the water column of lakes and that it is produced in the sediment (Rogers and Whitman 1991). Soils and grassland ecosystems are also sinks for methane and it has been estimated that the oxidation of methane from these sources has been reduced by 30% due to land use changes (Ojima et al. 1993). Soil sinks are significant as Duxbury (1994) suggests that if they were not present the level of atmospheric methane would rise at a rate 1.5 times its current level. Aerobic soils have been estimate to contribute to 15% of the global methane destruction (Goulding et al. 1996). Methane is used in the soils as an energy source for microorganisms such as methanotrophs, which oxidize methane to carbon dioxide, and nitrifiers, which oxidize ammonium to nitrate and also methane to carbon dioxide (Willison 1995). Soils with increasing amounts of nitrogen applied to them had decreasing ability to oxidize methane (Willison et al. 1995) which clearly shows that the way in which land is managed can affect the total methane sinks of the earth.

The oxidation of methane in the stratosphere is an important source of stratospheric water vapor (Willison et al. 1995). The following reaction involving methane and OH radicals converting into methyl radicals and water, accounts for the destruction of around 85% of the atmospheric methane. $CH_4 + OH \cdot \longrightarrow CH_3 \cdot + H_2O$ (Cicerone and Oremland 1988). The complete oxidation of methane is a series of reactions leading ultimately to water and carbon dioxide (Tyler 1991).

2.5 Factors influencing methane production in the ruminant

The two main factors affecting the amount of energy lost through methane are the amount of dietary carbohydrate consumed and the relative ratio of VFA produced in the rumen (Johnson and Johnson 1995).

Ruminal pH and rumen microbial population are both affected by the type of carbohydrate ingested. Lowered ruminal pH, which occurs with a high concentrate diet, inhibits growth of methanogenic bacteria (Demeyer and Henerickx 1967a). The type of carbohydrate affects the proportions of volatile fatty acids which are produced. If the acetic: propionic acid ratio is 0.5 then the loss of substrate carbon in the form of methane would be 0% whereas if all of the carbohydrate is fermented to acetic acid with no propionic acid formation, methane losses could be as high as 33% (Johnson and Johnson 1995).

Passage rates of digesta through the digestive tract will affect methane production with faster passages resulting in lower methane production (Okine et al. 1989). Methanogens are fastidious anaerobes (Tyler 1991) and cannot survive in the rumen if the dilution rate is too fast as they would have increased exposure to oxygen.

Many equations have been developed to predict the amount of methane produced by ruminants taking into account simple factors such as dry matter intake and more complex factors like physiological status of the animal and supplemental fat (Wilkerson et al. 1995). Blaxter and Clapperton (1965) described the relationship between feed digestibility and level of intake on methane production in the following formula:

$$Y_{CH4} = ((1.30 + 0.112\ D) + L\ (2.37 - 0.050D))/100 * GEI$$

Where Y_{CH4} is the amount of methane produced (Mcal/d CH_4) , L is a multiple of maintenance, and D is the energy digestibility of the feed determined at maintenance intake (% of gross energy). Wilkerson et al. (1995) examined several published equations for the prediction of methane from dairy cattle and found that for nonlactating cows, the Blaxter and Clapperton equation was the most accurate and precise predictor.

2.5.1 Methanogenic bacteria

Fermentation in the rumen results in the production of methane as an end product from methanogens which use H_2 to reduce CO_2 (formate) to CH_4. The majority of bacteria are classified in the lineage eubacteria. However, because of a 16S rRNA nucleotide sequence suggesting an early divergence from true bacteria (McAllister et al. 1996), methanogens are classified in the Archae domain of bacteria (formerly called Archaebacteria) (Darnell et al. 1990). This domain of bacteria includes those that live in unusual environments such as the halophiles which live in high concentrations of salt, and the thermoacidophiles which grow in hot (80°C) sulfur springs where a pH of less than 2 is common (Darnell et al. 1990). Out of the

sixty-six species of methanogens that have been identified from landfills, acidic peat bogs, waterlogged soils, salt lakes, thermal environments, and intestinal tracts of animals, only two are found in the rumen at numbers greater than 1×10^6 /ml (Rowe et al. 1979; Lovley et al. 1984a; Miller et al. 1986). These species are *Methanobrevibacter ruminantium* and *Methanosarcina barkeri*.

The production of methane in the rumen is a result of several steps and conversions of substances with the last step taking place by the methanogens (Fig. 2.2). Methanogens prevent the accumulation of hydrogen by reducing carbon dioxide to methane.

Methane producing bacteria most often utilize the substrates hydrogen, CO_2 and formate. Methanosarcina is an exception in that it utilizes methylamines, methanol, or acetate (Patterson and Hespell 1979; Whitman et al. 1992) to form methane. This allows them to flourish in diets containing molasses which promotes the utilization of methylamines, methanol, and acetate. Four mol of H_2 are used for the formation of one mol of CH_4 (Czerkawski 1986). The methane produced in the rumen is mostly disposed of through eructation (Immig 1996), with a small portion being absorbed into the blood stream and expired through the lungs (Murray et al. 1976).

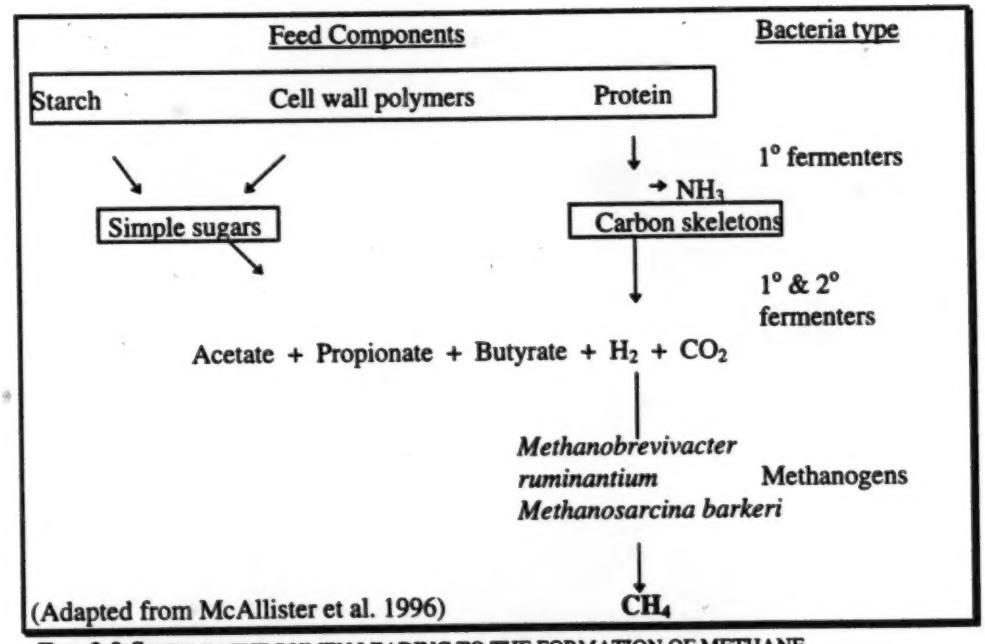

FIG. 2.2 STEPS IN THE RUMEN LEADING TO THE FORMATION OF METHANE.

2.6 Strategies to reduce rumen methane production

The importance of reducing methane production in ruminants from an environmental view is obvious, however, another good reason to examine possibilities of reducing methane emissions from ruminant animals is the loss of gross energy from the feed converted into methane and wasted. This can amount to anywhere from 2- 12% of gross energy in the feed (Johnson 1992).

As mentioned before, a shift in the ratios of volatile fatty acids with an increase of propionate, will result in a net decrease of methane production (Van Nevel and Demeyer 1996). This can be achieved by simple feed intervention with such things as feeding an increased proportion of easily fermentable carbohydrates by decreasing the amount of roughage in the diet (Cecava et al. 1990; Oshio et al. 1987);

lowered frequency of feeding, which has been shown to increase molar proportions of propionate (Sutton et al. 1986); and physical treatment of the feed such as grinding, pelleting and heating the feed which can increase the amount of propionate produced in the rumen (Moore et al. 1992).

Treating cereal straws with either NaOH or ammonia reduces methane production in sheep (Moss et al.1994). Maximum inhibition was found with wheat straw treated with ammonia. Methane is reduced by increasing the rate of degradation of organic matter, and reducing rumen retention time. The methane production declined from 58 L methane/kg of organic matter apparently digested (OMAD) with the untreated straw to 37 L/kg OMAD with the treated straw.

2.6.1 Ionophores

Feeding ionophores to ruminants reduces methane production in the short term by interfering with gram-positive bacteria, but the methanogens adapt with prolonged exposure (Chen and Wolin 1979; Rumpler et al. 1986). The extent of reduction depends on dose administered and ration fed (Van Nevel and Demeyer 1996). Two ionophores, monesin, and lasalocid, have both been shown to reduce methane production when added to feed of steers, but after two weeks the methane levels returned to original values (Rumpler et al. 1986).

2.6.2 Other chemical compounds

Compounds such as methylene blue, riboflavin, nicotinamide adenine dinucleotide, nitrate, sulfate, sulfite, methyl and benzylviologen reduce methane production *in vitro*, supposedly by supplying alternate electron acceptors to divert electrons from the reduction of CO_2 (McNeill 1957; Wolin et al. 1964).

Attempts to reduce methane by adding these compounds to the diet revealed that most of these compounds are not very specific and often resulted in excess H_2 gas production, so the usefulness of exogenous electron acceptors as a methane lowering technique is doubtful (Van Nevel and Demeyer 1996). The substance used for inhibition may have some toxic effects on the host animal i.e. hepatoxicity for chlorinated methane analogues (Lanigan et al. 1978).

Bromoethanesulfonate (BES) is a bromine analogue of coenzyme-M and thus inhibits the reduction of methyl-coenzyme M in methanogenic bacteria (Balch and Wolfe 1979). With recent investigations into the use of BES for the reduction of methane formation, it was found that methane levels initially decreased then began to rise after a period of 3 days, probably due to some sort of adaptation by the organisms (Immig et al. 1995). Although feed efficiency may be improved with decreased methane production, feed intake may decrease when such compounds are fed (Chalupa 1980).

2.6.3 Defaunation

The elimination of protozoa in the rumen through defaunation decreases methane production from 20-50% (Kreuzer et al. 1986; Williams and Coleman 1992). Some explanations for the decreased methane production in defaunated animals are the lower digestibility of crude fiber, the loss of methanogens attached to the ciliates, and the role of protozoa as producers of hydrogen and formate which are precursors of methane (see Fig. 2.2) (Van Nevel and Demeyer 1996). The problem with defaunation as an approach to reducing methane production, is that presently there is no satisfactory methods of defaunation (Kreuzer 1986).

2.6.4 Lipids

In an artificial rumen system (Dong et al. 1994), it was found that coconut oil (which contains high concentrations of C14:0) inhibited methane production in both a concentrate and a forage diets more than other oils such as canola and cod liver, which have high concentrations of unsaturated fatty acids. Since long chain fatty acids (LCFA) are toxic to not only methanogens, but also to protozoa and gram positive cellulolytic bacteria (Maczulak et al. 1981; Broudiscou et al. 1990), fiber digestion decreases when LCFA are added to the diet. This can be partially explained by the fact that with higher lipids in the diet (>5%), less organic matter and crude fiber is digested and digestion is shifted to the lower gastrointestinal tract where the efficiency of methanogenesis is much less (mol per mol of substrate fermented) than in the rumen (Demeyer and Degreave 1991).

Since some methanogens are attached to ciliate protozoa (Van Nevel and Demeyer 1996), the decrease in methane production following the addition of lipids to the diet could also be partially due to the lowered protozoa numbers found in the rumen after lipid addition (Czerkawski et al. 1975; Broudiscou et al. 1990).

2.7 Methods for determining methane production

Methane production is often obtained from measurements of respired air. This method involves measuring the flow of, and analyzing the composition of expired air from an animal and comparing it to atmospheric air. Differences in oxygen, carbon dioxide, and methane can be measured using specific analyzers. This is achieved by

having a mask or hood on the animal's head or by housing the animal in a metabolic chamber. The chamber must be relatively air tight and able to achieve a slight negative back pressure which ensures that any leaks will result in an inward flow not resulting in any loss of methane (Johnson and Johnson 1995). An advantage of the chamber over the hood is that it accounts for emissions resulting from both hindgut and ruminal fermentation. The usefulness of chamber data has been questioned because of the "unnatural" environment that the animal is exposed to. However, both statistical and modeling approaches for the relationship of energy intake to CH_4 production depend on respiration chamber studies (Johnson et al. 1994).

Methane production in dairy cattle has been measured in Ottawa from a barn with 118 cattle in it which was essentially made into a large calorimetry chamber where all the air exiting the building was analyzed for methane (Kinsman et al. unpublished). The average individual emission from the cattle was found to be in the range of previously published data for dairy cattle.

A recently developed method of measuring methane production, which has proven successful with cattle, is the sulfur hexaflouride(SF_6) tracer method. This method involves placing an evacuated collection canister on the neck of the cow with a tube running to the entry of the nostril to collect gases exhaled from the animal. A known amount of Sf_6, an inert gas, is placed in the rumen in a slow release capsule and is released at a known rate. From the amount of Sf_6 collected in the canister compared to methane in the canister, the amount of methane that was emitted from the animal can be calculated. Johnson et al. (1994) found this method to be accurate when compared to respiration chamber data. There is, however, the possibility of a

problem with this method if the canister is not adequate in size for the desired sample period because of the vacuum pressure will drop and the flow into the canister will slow down which would cause a non-uniform sampling rate.

2.8 Energy

2.8.1 Units

Energy, whether mechanical, electrical, or chemical, is measured in the SI system in units called joules. A joule can be converted into ergs, watt-seconds, and calories. A calorie is equal to 4.184 Joules, which is the energy required to raise the temperature of 1 g of water from 16.5° Celsius to 17.5° Celsius (NRC 1996). One thousand joules is equal to 1 kJ, and one thousand kJ is equal to one MJ. Since the energy of 1 joule is so small, either the kJ or the MJ are used when describing energy of feedstuffs for animals.

2.8.2 Partitioning of Energy

From an economic standpoint, the energy content of a feed and the energy requirement of the animal is the most important factor to consider when formulating a ration. An outline of energy partition is given in Fig. 2.3.

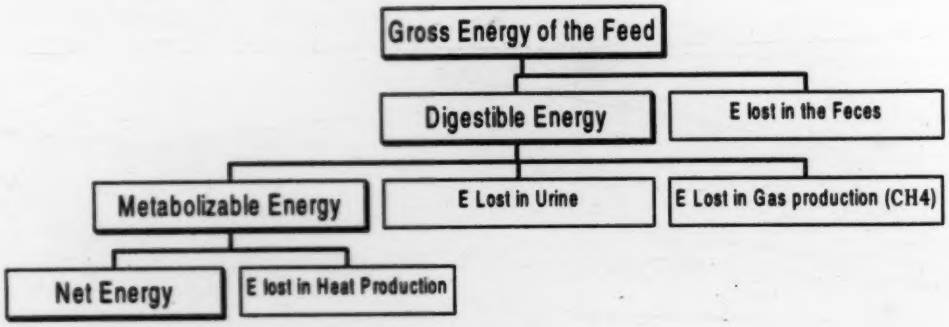

FIG. 2.3 PARTITIONING OF ENERGY IN AN ANIMAL.

2.8.2.1 Gross and digestible energy

The gross energy (GE) of feed is the energy per gram of feed determined by adiabatic bomb calorimetry. The digestible energy (DE) is the gross energy in the feed minus the energy lost in the feces of the animal, determined through fecal collection during digestion trials.

2.8.2.2 Metabolizable energy

Metabolizable energy (ME), is the digestible energy minus the energy lost in the urine and through gaseous (methane) losses. In cattle the ME is about 0.82 the DE, although the value is quite variable (NRC 1996). Ullrey et al.(1970) estimated that ME was 82.8% of DE in white-tailed deer fed a diet containing 17.6% crude protein, consisting of 34.7% corn ground, 29.5% corn, 18% soybean meal, and 10% linseed meal. This estimate was based on measured urinary loss and estimated methane loss based on cattle values. However, since for cattle methane losses are normally in excess of two times urine losses, not much reliance can be placed on Ullrey's estimate. Thompson et al. (1973) found the ME was 87% of DE in white-tailed deer fawns fed a concentrate diet based on corn meal with 6.75% alfalfa meal, and 16.8% protein. The gender of the fawn did not change this percentage. This study had the advantage of measured methane production and consequently is more accurate than the study by Ullrey (1970).

2.8.2.3 Net Energy

Net energy (NE) is the ME minus the energy lost through heat production associated with feed utilization (heat increment of feeding) (see Fig. 2.3). It can be

determined through either feeding trials where total energy changes in the body are measured or through metabolic rate determinations are made by indirect calorimetry.

2.9 Metabolic rate and Heat production

The basal metabolic rate (BMR) is a measurement of an animal's minimal rate of energy metabolism, which represents an approximation of the rate of metabolism of a fasting adult animal at rest in its thermal neutral zone (Gordon et al.1982). Since BMR implies a state of mental rest as well as not being influenced by food or temperature, it is a difficult state to achieve in wild animals and is more of a theoretical situation to be used in interspecies comparisons than an actual experimental unit of measurement. Fasting metabolic rate (FMR), determined after a 72 hour fast, is a more commonly used measurement of metabolism (Hudson and Haigh 1996). It is also referred to as the fasting heat production (FHP) of an animal. Resting metabolic rate (RMR) is the metabolic rate of animals at rest which have not been fasted and therefore includes the heat of digestion and nutrient metabolism. By the use of indirect calorimetry, fasting metabolic rate (FMR) can be determined which can then be used to determine the metabolizable energy (ME) for maintenance (ME_m) using efficiency factors of ME to net energy (NE). Information on FHP of various species is given in Table 2.3.

Table 2.3. Comparative daily fasting metabolic rates (kJ $kg^{-0.75}$ d^{-1}) for winter and summer and their corresponding calculated ME_m (kJ $kg^{-0.75}$ d^{-1}).

Species	Fasting Metabolic Rates (kJ $kg^{-0.75}$ d^{-1})		Metabolizable energy requirements for maintenance (kJ $kg^{-0.75}$ d^{-1})	
	Winter	Summer	ME_m Winter	ME_m Summer
Cattle	320	320	[a]480	[a]480
Domestic sheep	210	230	[a]315	[a]345
White-tailed deer	340	580	[b]578	[b]986
Mule deer	370		[b]629	
Red deer/Wapiti	365		[c]548	

(Adapted from Hudson and Haigh 1996)
[a] calculated using the cattle efficiency of conversion of NE_m to ME_m of 1.5 times FMR (AFRC 1990).
[b] calculated using the deer efficiency of conversion of NE_m to ME_m of 1.7 times FMR (Ullrey 1970).
[c] calculated using the red deer efficiency of conversion of NE_m to ME_m of 1.3 times FMR (Simpson et al. 1978).

Previously published values for metabolic rates of bison vary widely. The average winter resting metabolic rates of bison calves in winter was 461 kJ $kg^{-0.75}$ d^{-1} when fed a 50% concentrate 50% roughage diet at a level of 100g feed $kg^{-0.75}$BW (Christopherson et al. 1976). In a separate study, where bison were fed a 60% concentrate diet and 40% roughage at a level of 100g feed $kg^{-0.75}$BW, the metabolic rate was 718 kJ $kg^{-0.75}$ d^{-1} (Christopherson et al. 1979). Both studies took place in an environment of -30°C, and there is no simple explanation for differences between the two experiments.

2.9.1 Seasonal maintenance requirements estimated from feeding trials and indirect calorimetry

A seasonal effect on maintenance energy requirements can be seen in white-tailed deer in Table 2.4. The average winter value for white-tailed deer from is 540 kJ

$kg^{-0.75}$ and for wapiti is 550 kJ $kg^{-0.75}$ whereas the average summer values for white-tailed deer and wapiti respectively are 740 kJ $kg^{-0.75}$ and 860 kJ $kg^{-0.75}$.

The ME_m requirement for wapiti has been reported as 570 kJ $kg^{-0.75}$ d^{-1} for penned wapiti in the winter and 936 kJ $W^{-0.75}$ for grazing wapiti in the spring (Jiang and Hudson 1992). These values were obtained through a feeding trial where the ME was estimated as 82% of the digestible energy (DE). The spring value is double the maintenance requirements of other species but is close to the ME_m value of 986 kJ $kg^{-0.75}$ d^{-1} calculated for white-tailed deer using Ullrey's spring FMR value (1970). Temperature has been found to not have on effect on the digestive function of wapiti when digestibility trials were done on two groups of animals in two different temperatures at the same time of year (Westra and Hudson 1981).

The great difference between the spring and winter requirement for maintenance, in both deer and wapiti, shows the seasonality of maintenance requirement. Contrary to early conclusions about metabolic rate which suggested a decrease or slowing of the metabolic rate during the winter months, it is now thought that the energy requirements and metabolic rate increase above the interspecies mean during the spring and summer months for many northern wild ruminants (Hudson and Haigh 1996). The reason for a elevated summer energy expenditure may be to maximize growth during the period of abundant energy supply from plants.

Seasonality was also found with respect to average daily gain and intake in bison during a 266 day feeding trial where during some of the winter days 170 to 197 (Nov.- Dec.) they all showed a negative average daily gain and a lower intake, whereas during the rest of the trial they had a positive average daily gain (Stanton et

al. 1994). Response to shorter days and colder temperatures in winter appeared to overwhelm sensitivity to nutritional manipulation in this experiment (Stanton et al. 1994).

Table 2.4. Metabolizable energy requirements for maintenance (ME_m) for white-tailed deer and wapiti calculated through indirect calorimetry (IC) or feeding trials (FT).

	ME_m KJ/$Kg^{0.75}$/day	Source
	Winter:	
White-tailed deer		
Penned yearling females	548 FT	(Ullrey et al.1970)
Penned adult females	322-448 IC	(Worden and Pekins 1995)
Penned yearlings	523 IC	(Thompson et al. 1973)
Average:	**485**	
Wapiti		
Penned hinds	493 FT	(Jiang and Hudson 1994)
Penned hinds	573 FT	(Jiang and Hudson 1992)
Penned stags	570 FT	(Fennessy et al. 1981)
Penned calves	570 FT	(Cool 1982)
Average:	**550**	
	Summer:	
White-tailed deer		
Penned yearlings	803 IC	(Thompson et al. 1973)
Penned yearlings	678 IC	(Holter et al. 1979)
Average:	**740**	
Wapiti		
Penned hinds	728 FT	(Jiang and Hudson 1994)
Grazing hinds	900 FT	(Jiang and Hudson 1994)
Grazing hinds	936 FT	(Jiang and Hudson 1992)
Grazing stags	878 FT	(Wairimu et al. 1992)
Average:	**860**	

2.10 Digestive Physiology of Wild Ruminants

With the rise of game farming particularly in Alberta, research into digestive properties and energetic efficiency of feed utilization, including the loss of energy as methane, in wild ruminants is increasingly important. This and environmental

concerns are both rationale for the examination of methane production by farmed wild ruminants.

2.10.1 Digestive strategies

Three commonly farmed species of wild ruminant in Alberta are white-tailed deer, bison, and wapiti. Every species of wild ungulate has unique digestive characteristics which are the basis for a classification scheme by Hofmann (1989). Wapiti have been described as an intermediate or mixed feeder which selects a mixture of food from grasses to browse leaves. White-tailed deer have been described as concentrate selectors which select a diet of browse such as leaves and shrubs exclusively. Bison are on the other end of the scale and are classified as roughage/grass eaters which select a roughage-type food such as grass.

A trade-off occurs when examining the strategies of different species. Roughage/grass eaters keep their food in the rumen for a long time to ensure complete digestion of the highly lignified, fibrous material which they consume. Their digestive system is characterized by a smaller relative stomach size than that of concentrate selectors and an omasum which is capacious and extensively subdivided (Hofmann 1988). The diet of a roughage eater-grazer is more fibrous than the diet of a concentrate selector. One of the adaptive features that Hofmann identifies in grazers is selective retention of large particles in the rumen. Particle sizes larger than 0.5 mm are selectively retained in the rumen of sheep (Hofmann 1989). This limits food intake by keeping the rumen full until very complete digestion occurs. A concentrate selector, such as the white-tailed deer, keeps feed in the rumen for a shorter time enabling digestion of quickly digestible nutrients, which makes gut fill less of a factor

in voluntary feed intake. The digestive tract of concentrate selectors are characterized by stomachs with the smallest relative weight and capacity, the least subdivision, and the largest openings of all the ruminant feeding types (Hofmann 1988). The concentrate selector's omasum is relatively small and reticulum is proportionally much larger than that of grass/roughage eaters (Hofmann 1988). The diet of a concentrate selector or browser is more easily fermented and therefore the animal digests feed only to the point where further digestion would result in an energy loss rather than gain.

Hofmann (1989) states that body size is unimportant with respect to feeding type since there are concentrate selectors which have large body size and grazers with small body size and vice versa. Prins et al. (1984) have shown that the rate of cellulose digestion is lowest in concentrate selectors regardless of body weight, which tends to support the Hofmann hypothesis.

Also in support of Hofmann's hypothesis, are the results from a study by Henke et al. (1988) where the relative rumen capacities (by weight) of axis deer (*Axis axis*), white-tailed deer, blackbuck antelope (*Antilope cervicapra*), sika *deer (Cervus nippon*), and fallow deer (*Dama dama*) where examined. They found that white-tailed deer and axis deer did not differ significantly in their relative rumen capacity. White-tailed deer are classified as concentrate selectors and axis deer are classified overlapping the concentrate selector and intermediate feeder type (Hofmann 1985). Sika and fallow deer overlap the intermediate feeder and grass-roughage eater category. They were found to have significantly higher relative rumen capacities. Blackbuck antelope had the highest relative rumen capacity and are classified as

overlapping in the intermediate feeder and grass-roughage eater category (Hofmann 1988).

In contrast to the above hypothesis, both Gordon and Illius (1994) and Robbins et al. (1995) suggest that it is not differences in digestive anatomy that account for digestion patterns among groups of wild ruminants, but rather body size. When comparing 8 browsers, 7 intermediate, and 11 grazing African ruminants mean retention time, Gordon and Illius (1994) stated that 99.6% of the variance was explained by a model with body mass and food type. Robbins et al. (1995) argue that both flow rate of liquid from the rumen and fiber digestion are strongly related to body weight. Robbins (1995) recognized that the parotid glands are normally three to four times larger in concentrate selectors (1.4-2.2 g kg^{-1} body weight (BW)) than in roughage eaters (0.5-0.7 g $kgBW^{-1}$) (Kay 1987 1989) which would tend to support Hofmann's hypothesis. However, Kay (1987) found little difference between ruminant species in resting salivary secretion rate, which for wapiti is about 0.4-0.5 ml $kg^{-0.75}$ min^{-1}. A lack of difference in saliva production is consistent with the body weight hypothesis proposed by Robbins et al. (1995). Robbins (1995) also suggested that perhaps as a result of smaller bite sizes, more saliva would be swallowed per bite by concentrate selectors but he argued that body size would explain this difference rather than digestive differences. However since the Kudu, which is a browser, has both grazer sized parotid glands, and absence of tannin binding proteins, it is apparent that it cannot be assumed that all concentrate selectors have more tannin binding proteins in their saliva than grazers which appear to help defend to animal against plant secondary compounds (Austin et al. 1989).

2.10.2 Digestibility of diets by different ruminants

Digestibility for various animal species and experiments is analyzed in Table 2.5. Few experiments have been published in which more than one species of native ungulate have been compared. It would appear, though, that digestion of grass hay might be higher in wapiti than mule deer (Baker and Hansen 1985). Mould and Robbins (1982) found that the major difference in digestibility between wapiti and white-tailed deer occurred at the lower lignin-cutin concentrations of less mature forages and that the longer retention time in the larger ruminant would allow for more complete digestion of available fiber. These studies are supported by an *in vitro* study of digestion between cattle, goats, nilgai, and white-tailed deer, where it was found that deer inoculate was the least efficient and that the difference seemed to be a result of their lower ability to digest fiber (Priebe et al. 1987). The mean digestibility found in the literature for white-tailed deer, cattle and wapiti was 55.2%, 63.1%, and 61.3% respectively (Table 2.5).

Thus, although reasons for differences in digestive physiology between the various wild ruminants are unclear, each species appears adapted to it's type of diet and that differences in efficiencies in feed utilization might be expected between species. With such variation in the natural diet selection and strategy of digesting it, grouping all wild ruminants together when estimating their global contribution to the greenhouse effect through methane production, is very inaccurate. More accurate estimates of methane production from these animals are therefore needed.

Table 2.5. Dry matter digestibilities of ruminants

Feed type	Bison	Cattle	Wapiti	Mule Deer	Red Deer	Sheep	White-tailed deer	Source
ad lib alfalfa hay	77.5	-	-	-	-	-	-	2
ad lib alfalfa hay	-	-	-	-	-	-	55.2	7
ad lib alfalfa hay	-	63.1	-	-	-	58.1	-	6
ad lib alfalfa hay	-	-	61.3	-	-	-	-	5
ad lib brome hay	-	-	-	-	-	-	54.4	7
ad lib brome hay	-	-	48.3	-	-	-	-	5
ad lib brome hay	-	-	62.1	57.1	-	-	-	1
ad lib lucerne hay	-	-	-	-	56.0	55.0	-	3
Grass hay/barley	-	-	-	-	56.0	-	-	8
hay adlib	-	-	-	-	54.0	58.0	-	4
wildlife pellet	-	63.4	-	-	-	-	56.6	6
Average	77.5	63.4	57.2	57.1	55.3	57.0	55.4	

1 Baker and Hansen 1985
2 Christopherson et al. 1976
3 Domigue et al. 1991
4 Kay and Goodall 1976
5 Mould and Robbins 1982
6 Priebe et al. 1987 -*in vitro* study
7 Robbins et al. 1975
8 Sibbald and Milne 1993

2.10.3 Mean retention time

Mean retention times of digesta in the digestive tract of wapiti, red deer, and sheep are given in Table 2.6.

Table 2.6 Mean retention times (MRT) of digesta in the digestive tract of various ruminants

Species	Feed (level and type)	MRT (hours)	Source
Wapiti	90% *ad lib* alfalfa pellet	68-80	Dean et al. 1980
	90% *ad lib* alfalfa baled	120-140	Dean et al. 1980
Red deer	*ad lib* hay	54	Kay 1976
	ad lib grass hay barley conc.	33.7[W]	Sibbald and Milne 1993
	ad lib grass hay barley conc.	33.4[S]	Sibbald and Milne 1993
Sheep	*ad lib* hay	62	Kay 1976

[S] Summer [W] Winter

There is essentially no information on digestion and passage rates in deer and bison. It might be expected that concentrate selectors, such white-tailed deer, with a

natural diet consisting of more highly digestible food, would have faster passage rates through the digestive tract and thus have lower methane production since in cattle it has been found that as passage rates increased, methane production decreased (Okine et al. 1989). Bison, which consistently select lower quality forages than cattle (Towne et al. 1988) have been observed to have lower retention times than cattle (Young et al. 1977) which would result in more methane per kg of feed consumed than cattle. In the study by Kay et al. (1976) shown in Table 2.6, the mean retention time is lower in red deer than in sheep. Since red deer, wapiti and sika deer are all classified as intermediate feeders by Hofmann (1988), it would be expected that wapiti would have similar methane production as reported for sika deer.

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3. Methane Production in Native Ruminants

3.1 Introduction

Three commonly found species on game farms in Canada are white-tailed deer (*Odocoileus virginianus*), wapiti (*Cervus elaphus*), and bison (*Bison bison*). Animal populations on game farms in Canada have increased to about 19144 wapiti, and 7039 white-tailed deer at the end of 1995 (Houdepohl 1997). Numbers of farmed bison are more difficult to determine since there is no mandatory registry as there is for white-tailed deer and wapiti. However, it was estimated that in 1996 there were around 28000 bison in Alberta, with Alberta's bison making up approximately 50% of the farmed population in Canada (Houdepohl 1997).

These species differ substantially in their strategy of digestion. Bison, wapiti and white-tailed deer have been classified by Hofmann (1989) as roughage/grass eaters, intermediate/mixed feeders, and browse/concentrate selectors, respectively, based on their predominant natural diet. The basis for the classification scheme is differences in the digestive tract which better equips each group to digest it's type of diet. For example, concentrate selectors have the smallest relative stomach size, least subdivision, and the largest openings between the stomach compartments compared to grass/roughage eaters (Hofmann 1988). It is therefore expected that there would be differences in digestion and efficiencies of feed utilization between these species.

One source of inefficiency of feed utilization in ruminant animals is the loss of gross energy intake to gas as methane. Methane is the second largest contributor to the greenhouse effect and has been estimated to contribute 18% to the overall greenhouse effect (Leng 1990). Its atmospheric concentration has increased from the

estimated pre-industrial revolution level of 0.7 to 1.7 ppm, which was the level in 1989 (Tyler 1991). Anaerobic microorganisms in ruminant animals have been estimated to produce about 80 Tg of methane each year, which is about 16% of the total annual global emission of 515 Tg (Watson et al. 1992). The wild ruminant population in temperate regions of the world has been estimated by Crutzen et al. (1986) to produce 0.37 Tg/yr of methane. This is however likely a high estimate since it was calculated using the assumption that 9% of gross energy (GE) intake is lost as methane. This estimate is high, even for cattle, but methane production has not been measured previously in bison, wapiti, or white-tailed deer.

The objectives of the present research was conducted to measure and compare methane emission from three wild ruminants, bison (*Bison bison*), wapiti (*Cervus elaphus*), and white-tailed deer (*Odocoileous virginianus*), and to test the hypothesis that the proportion of feed energy lost as methane between these species is greatest in bison which are grazers, lowest in white-tailed deer which are browsers, and intermediate in wapiti which are mixed feeders.

3.2 Methods

The experiment consisted of two periods, the first from March to April 1995 and the second from May to June 1995. During each period feed digestibility was determined and O_2 consumption and CH_4 production were measured by indirect calorimetry. In addition, mean retention time of liquid and particles in the total digestive tract were estimated using CoEDTA and chromium mordanted fiber respectively. The latter data is not presented in this thesis.

3.2.1 Study area, animals, and diet

This study took place at the University of Alberta Ministik Wildlife Research Station in the Cooking Lake moraine approximately 50km SE of Edmonton, Alberta.

All of the procedures were approved by a University animal care committee and a veterinarian was consulted for any questions on nutrition and animal welfare. Five female bison (195.7 ± 23.8 kg), five female wapiti (151.3 ± 13.0 kg), and eight female white-tailed deer (34.9 ± 4.62 kg) were used for the study. All the animals were approximately 1 yr. old. The bison and wapiti were selected from a herd based on similar weights. The bison were yearling calves brought to Ministik from Elk Island National Park east of Edmonton, Alberta. The wapiti herd at Ministik were first introduced in August 1977 from a herd at the Sybille Research station, Wyoming. The herd has been supplemented with stags from nearby Elk Island National Park for breeding in recent years (Hudson 1987). The white-tailed deer were brought to Ministik in the spring of 1994 as orphaned fawns that had been turned in to Fish and Wildlife (Alberta Environmental Protection).

Animals were fed sun-cured alfalfa pellets *ad libitum* (*ad lib*) throughout the entire experiment.

3.2.2 Digestibility trials

The animals were adjusted to the feed for a minimum of 2 weeks prior to the commencement of each periods. During this time average group feed consumption of the animals was recorded daily and an average group intake rate was calculated using the intakes from the last 5 d of each of the two adjustment periods.

Immediately before the digestibility period animals were weighed using a platform scale (Accurate Scale Industries Ltd. Model #DF1000, Vancouver). The animals were penned individually to measure individual feed consumption and to accustom them to being by themselves 24 hr before the animals were put in the collection crates (2.32m X 1.19m X 1.64m). The animals had been exposed to the collection crates at least once before the digestibility measurements were made, by holding them in the crates for a minimum of 3 hr. The collection crates had a mesh floor to catch the feces and separate the material from the urine which was collected in a tub below the floor. Digestibility measurements were made over a 5 d period with the first wk of measurements beginning on March 6, 1995 for the first period and on May 1, 1995 for the second period. The animals were put randomly into the crates with at least one animal/group of each species put into the five crates each week. The white-tailed deer were put into the crates in pairs to reduce stress associated with being penned separately.

During each of the digestibility trials, orts were collected and feed given between 0900 to 1000 h. Water was given ad libitum whenever necessary.

Representative samples of each were collected and transferred to a freezer at -20^0 C until further analysis. Any hair in the feces was removed with a nail comb and the remainder was removed manually before laboratory analysis.

3.2.3 Methane production and oxygen utilization

After the animals completed the digestibility trials they were returned to the herd. Prior to respiration measurements they were penned individually for individual feed consumption determination 24 hrs before going into the metabolic crate. The calorimetry measurements began, in both periods, in the week following the digestibility trials. In period one, the last animal finished calorimetry in the first week of April, and in the second period the last animal finished calorimetry in the first week of June. Outside air temperatures were obtained daily with a maximum-minimum thermometer during the respiration measurements.

For methane and oxygen measurement, wapiti and bison were held in a chamber identical to the digestibility crates with the exception of a sealed solid floor while the deer were put into a smaller crate (1.00 m x 1.44 m x 1.83 m), which was otherwise identical to the digestibility crates, including the mesh floor. The animals were left in the chambers for a total of 30 hr and data was collected for the final 24 hr. Air was continuously withdrawn from the chamber, and gas flow, temperature, pressure, and O_2 and CH_4 concentration were all monitored. Flow rates were adjusted to try to maintain of oxygen concentration in the chamber of approximately 20%, with an average flow rate over both periods of all species, of 95.36 L min^{-1}. The air was dried through Drierite (W.A. Hamond drieritte Co. Ltd. Xenia, Ohio) to remove H_2O before entering gas analyzers. The oxygen analyzer (Servomax model 540A) and the

methane analyzer (Rosemount Analytical Model 880A, Rosemount CA) were calibrated at the beginning of each 24 hr measurement. Nitrogen gas was used to zero both analyzers, span gas (19.18% O_2, 0.0995% CH_4) was used to set the oxygen and methane analyzer's mid range, and atmospheric air was used to set the O_2 analyzer's upper end (20.95% O_2 ; Maclean and Tobin 1987). The data was collected every second and then averaged over 60 seconds by a Data Taker (Data logger DT100, data electronics, Australia) and then transferred to a computer using software designed to record the information (Datagrabber, designed by G. Godby and P. Gregory at the University of Alberta).

To determine the accuracy of the system, a known amount of nitrogen was released into the chambers. A full bottle of nitrogen was weighed (mean weight of 5523.2g) and then placed into the chambers and nitrogen was released over a known time period (10 min). The derived recovery factor was then used to adjust all measurements of gas flow.

3.2.3.1 Calorimetry Calculations

Heat production (HP) was determined using the formula $M = -20.5V_E\Delta Fo_2$ (Maclean and Tobin 1987) where M is the metabolic rate in kW (1kW=1kJ sec^{-1}), V_E is the expired flow rate at standard temperature and pressure for dry air in L sec^{-1}, and ΔFo_2 is the difference in O_2 concentrations by volume between inspired and expired air (F_E-F_I). Methane was converted to kg using the relationship 1 L CH_4 = 0.716 g (Maclean and Tobin 1987) and to energy equivalents by the relationship 1 L CH_4 = 40kJ (CRC 1978).

Metabolizable energy requirement for maintenance (ME_m) was estimated using the determined ME intake (MEI) and HP values and estimation of fractional efficiency of utilization of metabolizable energy for maintenance (k_m) and gain (k_g) according to the following equation: ME_m= MEI - ER/K Where ME_m= metabolizable energy required for maintenance (kJ $kg^{-0.75}$), ER= energy retention (kJ $kg^{-0.75}$) and K= fractional efficiency of conversion of ME into net energy. The ER can be calculated as MEI -HP. The above equation can therefore be expressed as ME_m= MEI + ((HP - MEI) * $100/k_m$) if HP is greater than MEI and ME_m = MEI - ((MEI - HP)*($100/k_g$)) if HP is less than MEI. Cattle efficiencies (k_m = 63.3% ; k_g = 38.5% ; NRC 1984), which corresponded to the ME content of the diet of 8.4 MJ kg^{-1} (NRC 1984), were used. In addition, a value of 67% for k_g was used for all species based on Jiang and Hudson (1992), and the same efficiency (k_m=63.3%) was used for maintenance.

3.2.4 Laboratory analysis

Feed and fecal samples were dried to a constant weight at 100^0C and ground through a 1mm mesh screen with a Thomas Wiley laboratory mill (model 4, Philadelphia, USA). They were then analyzed for DM, ash, nitrogen content, fiber (neutral detergent fiber (NDF), acid detergent fiber (ADF), and lignin), and gross energy (GE). Hydochloric acid (1% by weight) was added to urine samples to minimize nitrogen losses and then the samples were freeze-dried (Virtis company 50-SRC freeze dryer, Gardiner NY) before analysis.

Nitrogen was determined by the Kjeldahl procedure (Assoc. Off. Anal. Chem. 1980) and gross energy by adiabatic bomb calorimetry (Leco automatic calorimeter

AC 300, St. Joseph MI) (Procedure No.). Lignin, ADF, NDF and ash concentrations in feed, feces and orts by procedures given by Van Soest and Robertson (1980).

3.2.5 Statistical Analysis

Data were analyzed using the GLM and LSMEANS procedure in SAS (Schlotzhauer and Littell 1987) with comparisons for significant differences made by the probability of differences (PDIFF) option. The data were analyzed as a split plot design with animal nested within species as an error term for species. Differences between species, season (trial date), and their interaction were examined. The equation used as the model statement in the analysis was as follows:

$$Y_{ijkl} = \mu + Sp_i + A(Sp)_j + S_k + I_l + e_{ijkl}$$

Where Y is the dependent variable; μ is the overall mean; Sp_i is the species effect; $A(Sp)_j$ is animal nested within species effect; S_k is the season (or time period) effect; I_l is the interaction between season and species effect; and e_{ijkl} is the residual error.

3.3 Results

3.3.1 Feed

The suncured alfalfa pellets averaged 95.2% DM, 18.1 kJ g^{-1} gross energy content, 13.9% protein, 59.2% NDF, 43.5% ADF, and 11.1% lignin on a dry matter basis. There was no difference in composition of the orts (values not shown) compared to the feed which indicates the uniformity of the feed prevented animal selection.

3.3.2 Environmental temperature

The mean outside temperature during the first period was +0.6°C and during the second period was +7.0°C.

3.3.3 General health of the animals

Despite the stress associated with being isolated in crates, the animals faired well through the experiment. There was one pair of deer whose intake was very low during the digestibility trial and therefore their data was not used in the calculations of digestibility or voluntary intake in either the pre-digestibility period or during the digestibility trial. During the calorimetry trial one bison had a very low intake and thus its data was also not used.

The alfalfa pellets were readily eaten by wapiti and bison but were not as palatable for the deer. Generally it took the deer a longer time to adjust to the feed and to reach a constant daily intake. Also, they were observed chewing on the hair of other animals. This could have been a nervous response, but is more likely a response to not having browse material to chew on since it occurred both in the group pens as well as in the digestibility crates. The natural diet of white-tailed deer includes several

different types of browse including balsam popular, bearberry, juniper, rose, willow, alfalfa, aster and blue bells (Stelfox 1993) so pelleted alfalfa as a sole dietary source for deer is somewhat unnatural.

3.3.4 Handling considerations

Although the deer were bottle-raised and had plenty of exposure to humans, they were not very tame during the trials. Indicators that the deer were stressed other than the above mentioned, were the relatively low intake and the low to negative nitrogen balance obtained during the digestibility trials. The deer varied in their response to handling as some of them appeared quite relaxed throughout most of the handling and trials, whereas others appeared to lose weight and were very jittery. Pairing the deer did not totally alleviate the problem of stress, and there may be no need for this in future trials. The fact that they were stressed may have had an impact on the results of this experiment, and could partially explain why many measurements made with the deer were more variable than with the other two species.

The bison also became quite worked up when handled and put into the crates, however, they settled down more quickly than did the deer and seemed more calm and content once they were in crates. There were generally less variation in bison than deer data.

Wapiti were by far the most even-tempered species of the three and gave the most consistent and reliable results with the least variation. They were predictable and intelligent during their handling and were the most adaptable to the experimental conditions of the crates.

3.3.5 Ad libitum intakes

Numerically, the highest dry matter intake (DMI) for bison were measured in the group feeding situation, few differences in intake with measurement times were detected with wapiti, and the highest intake for deer was observed when they were held in crates (Table 3.1).

Intakes while the animals were in groups combined over both measurement periods, of 111, 86, and 46 g $kg^{-0.75}$ for bison wapiti and deer, respectively (Table 3.1). Significant differences were observed between species during both the pre-digestibility and digestibility periods. Bison consumed 61% more than deer ($P = 0.02$) during the pre-digestibility period and wapiti consumed more than either bison or deer ($P < 0.05$) during the digestibility trial. No DMI differences between species were detected during calorimetry measurements (Table 3.1). There was a significant month effect on DMI in all of the measured intakes. In all cases the higher intake occurred during the April-May measurement period ($P < 0.01$).

There were significant interactions ($P < 0.01$) between species and date of measurement in both the pre-digestibility and pre-calorimetry DMI data. Wapiti increased their intake in the May period more than either bison or deer; during the pre-digestibility DMI measurements the DMI of wapiti was more than 3.5 times their intake in March.

3.3.6 Digestibility and Urinary Output

From Table 3.2 it can be seen that there were no differences ($P < 0.05$) in digestibility of DM or any feed constituent between species, month of measurement,

or their interaction. However, there were trends ($P < 0.10$) for OM, NDF, and ADF digestibility to be higher in wapiti than in deer.

A species effect on nitrogen balance was evident with deer retaining less ($P < 0.01$) nitrogen than either wapiti or bison. More nitrogen was retained in May than in the March period. There was also a species by date interaction ($P < 0.03$) with the bison and wapiti both retaining more nitrogen in May, and deer exhibiting no difference between periods but having lower retention's than either bison or wapiti in both measurement periods.

Urinary energy loss ($kJ \cdot d^{-1}$) was significantly higher in both the bison and wapiti than in the deer.

3.3.7 Methane production

In Table 3.3, methane, heat production, digestible energy intake (DEI), MEI, and calculated maintenance values are reported. There was a marked species effect on methane production with the ranking between species as follows: bison > wapiti > deer. A seasonal effect was evident for methane production with more methane production in March than in May except when expressed as CH_4 L d^{-1}, where the same trend was evident but not significant. Methane lost expressed both as a percentage of gross energy intake (GEI), and in relation to DMI, showed a species by date interaction at the $P = 0.06$ level with the deer exhibiting little difference between the March and May value.

3.3.8 DE and ME content of diet

There was trend for a species ($P < 0.10$) in concentration of DE in the diet and the ratio of ME to DE (Table 3.4); deer showed a lower dietary DE than both bison

and wapiti determined at ad libitum intake. Measurement date and the species interaction with the measurement period had no affect on the DE or ME content of the diet. An effect of date on the ME:DE ratios was present ($P < 0.01$) with ratios being being higher in the May measurement period than in March.

3.3.9 Digestible and metabolizable energy intakes

In Table 3.3, a species effect on digestible energy intake (DEI) can be seen, with deer having a higher DEI than bison ($P < 0.05$). The combined season effect is also significant ($P < 0.01$) with the higher intake occurring during the second measurement period. There was a trend ($P = 0.06$) for wapiti and to deer increase in DEI more in May than bison.

No species differences were detected in metabolizable energy intake (MEI) (Table 3.3). There was however a seasonal effect with MEI in the May measurement period higher ($P < 0.01$) than in the March period. No significant species by date interaction for MEI was seen (Table 3.3).

3.3.10 Heat production and estimated maintenance requirements

No species effect were found for heat production. A seasonal effect ($P<0.03$) for all three species combined was evident with greater heat production in the May period. No species by date interaction was found for this parameter.

No significant differences or interactions were observed for the estimates maintenance requirements.

Table 3.1 Body weight and Ad libitum intakes of alfalfa pellet dry matter (DMI) at different times in the experiment.

Date and Species	Weight (kg)	Group DMI g kg$^{-0.75}$	--Digestibility-- Pre-trial g kg$^{-0.75}$	Days 1-5 g kg$^{-0.75}$	--Calorimetry-- Pre-trial g kg$^{-0.75}$	During trial g kg$^{-0.75}$
Species						
Bison	195.7 ± 7.52[z]	111.5 ± 6.1	98.5[a]	69.7[b]	89.3	77.7
Wapiti	151.3 ± 4.1	86.3 ± 8.3	78.4[ab]	87.1[a]	82.7	89.7
Deer	34.4 ± 1.45	46.4 ± 2.8	61.1[b]	67.7[b]	68.8	92.9
SE[y]			7.3	5.3	11.3	5.0
Prob[x]			0.02	0.05	0.51	0.18
Date (1995)						
Feb, March	133.4 ± 16.32	67.6 ± 6.8	51.7[b]	53.7[b]	65.0[b]	72.4[b]
April, May	141.2 ± 21.05	95.21 ± 9.4	106.9[a]	95.9[a]	95.6[a]	101.2[a]
SE			3.0	4.2	4.6	3.8
Prob			0.00	0.00	0.00	0.00
Species x Date						
2-03 Bison	177.4 ± 6.10	97.5 ± 6.9	82.5[b]	55.1	82.9[ab]	69.9
2-03 Wapiti	149.1 ± 2.88	62.1 ± 3.0	33.5[c]	55.7	46.4[b]	69.2
2-03 Deer	33.9 ± 2.86	43.2 ± 3.3	39.2[bc]	52.7	65.6[ab]	78.0
4-05 Bison	212.4 ± 7.04	125.5 ± 4.8	114.5[a]	84.4	95.7[a]	85.6
4-05 Wapiti	153.4 ± 8.06	110.5 ± 3.1	123.2[a]	118.5	119.0[a]	110.2
4-05 Deer	34.8 ± 2.54	50.0 ± 4.2	82.9[b]	84.9	72.0[ab]	107.9
SE			22.4	13.2	24.6	8.4
Prob			0.00	0.08	0.01	0.25

[z] Values following means are standard errors of mean animal intake of animals kept in groups. There were eight deer, five bison and five wapiti in the pens from which the measurements came from for both time periods.

[y] SE = Standard error, [x] Prob = Probability .

[a - c] Means in the same column and comparisons not followed by the same superscript differ significantly ($P < 0.05$).

Table 3.2. Least squares means of digestibility, and nitrogen balance in bison, wapiti, and deer fed sun-cured alfalfa pellets

Date and Species	DM[z] %	OM[z] %	E[z] %	N[z] %	NDF[z] %	ADF[z] %	N B[z] g/d	Urine kJ/d
Species								
Bison	48.9	52.9	51.0	58.7	39.1	35.4	27.1[a]	1064[a]
Wapiti	51.2	54.1	51.2	57.0	44.0	41.3	27.3[a]	1124[a]
Deer	46.9	49.1	46.4	56.6	37.2	32.7	1.7[b]	454[b]
SE[1]	1.8	1.4	1.6	2.0	2.0	2.2	2.9	63.0
Prob[1]	0.30	0.10	0.15	0.71	0.10	0.07	0.00	0.00
Date								
March 1995	49.4	52.3	50.0	56.0	41.3	38.1	8.7[b]	701[b]
May 1995	48.6	51.7	49.1	58.9	38.8	34.9	28.7[a]	1061[a]
SE	1.1	1.0	1.1	1.6	1.3	1.4	2.3	68.3
Prob	0.61	0.64	0.57	0.27	0.19	0.16	0.00	0.01
Species x Date								
March Bison	49.1	53.0	51.0	56.9	41.2	37.7	11.9[b]	939
March Wapiti	53.5	56.2	53.8	55.9	47.1	45.4	14.4[b]	807
March Deer	45.6	47.5	44.2	55.8	36.0	31.2	-0.3[c]	358
May Bison	48.7	52.8	51.0	60.5	37.1	33.2	42.3[a]	1190
May Wapiti	49.0	51.9	48.5	57.2	40.9	37.2	40.1[a]	1443
May Deer	48.1	50.3	47.6	58.9	38.4	34.2	3.7[c]	550
SE	2.3	2.2	2.7	1.0	2.8	3.6	8.8	169.3
Prob	0.28	0.24	0.17	0.89	0.24	0.17	0.03	0.18

[z] Abbreviations: ADF = Acid detergent fiber, DM = Dry matter, DMI = Dry matter intake, E = Energy (kJ), NB = Nitrogen balance, NDF = Neutral detergent fiber, Prob = Probability, SE = Standard error. Based on eight deer, five bison, and five wapiti.

[a - c] Means in the same column and comparisons not followed by the same superscript differ significantly ($P < 0.05$).

Table 3.3. Least squares means of methane production, heat production, and calculated metabolizable energy requirements for maintenance (ME_m) in bison, wapiti, and white-tailed deer.

Date and Species	Methane Production				HP[z] and intake (kJ/kg$^{0.75}$)			Calculated ME_m	
	L/d	L/kg DMI[z]	L/kg dig. DMI	CH_4 % of GEI[z]	DEI[z]	MEI[z]	HP·d^{-1}	Cattle (K_z =)	Wapiti (K_z =)
Species									
Bison	121[a]	30.1[a]	62.7[a]	6.6[a]	638[b]	514	652	699	734
Wapiti	87[b]	23.5[b]	45.4[b]	5.2[b]	798[ab]	691	698	618	708
Deer	33[c]	15.0[c]	32.5[b]	3.3[c]	904[a]	783	884	685	868
SE[z]	10	2.6	4.0	0.6	65	65	154	254	215
Prob[z]	0.00	0.01	0.00	0.01	0.05	0.08	0.58	0.97	0.87
Date									
March 1995	83	27.9[a]	55.8[a]	6.2[a]	566[b]	439[b]	608[b]	605	650
May 1995	78	17.9[b]	39.4[b]	3.9[b]	994[a]	886[a]	881[a]	730	890
SE	6	1.5	3.5	0.32	29	23	74	160	118
Prob	0.57	0.00	0.01	0.00	0.00	0.00	0.03	0.62	0.22
Species x Date									
March Bison	136	38.8	77.7	8.6	502	322	565	706	706
March Wapiti	84	29.1	54.1	6.4	535	438	593	683	683
March Deer	29	15.9	35.5	3.5	661	558	665	426	560
May Bison	106	21.5	52.0	4.7	774	707	739	693	763
May Wapiti	91	18.0	36.7	4.0	1060	943	801	553	733
May Deer	36	14.2	29.5	3.1	1148	1008	1103	944	1176
SE	13.4	5.1	7.7	1.1	99	40	97	221	203
Prob	0.20	0.06	0.25	0.06	0.06	0.40	0.58	0.54	0.40

[z] Abbreviations: DMI = Dry matter intake, DEI = Digestible energy intake, GEI = Gross energy intake, HP = heat production, K_z = efficiency of ME use to gain, MEI = Metabolizable energy intake, Prob = Probability, SE = Standard error. Based on eight deer, five bison, and five wapiti.

[a-b] Means in the same column not followed by the same superscript differ significantly ($P < 0.05$).

Table 3.4 Mean digestible energy (DE) and metabolizable energy (ME) content of diet, and ME:DE ratios for bison , wapiti, and white-tailed deer at *ad libitum* intake during digestibility trial

Date and Species	Diet DE (MJ kg^{-1})	Diet ME (MJ kg^{-1})	ME:DE
Species			
Bison	9.2	7.2	0.79
Wapiti	9.2	7.9	0.85
Deer	8.4	7.2	0.85
SE[z]	0.28	0.30	0.02
Prob[z]	0.08	0.35	0.10
Date			
March 1995	9.0	7.1	0.78[b]
May 1995	8.9	7.8	0.88[a]
SE	0.17	0.29	0.02
Prob	0.19	0.15	0.00
Species x Date			
March Bison	9.2	6.5	0.70
March Wapiti	9.7	7.9	0.81
March Deer	8.1	6.8	0.83
May Bison	9.2	7.9	0.88
May Wapiti	8.8	7.8	0.89
May Deer	8.6	7.6	0.88
SE	0.49	0.48	0.04
Prob	0.17	0.41	0.14

Note: The dietary GE for above was 18.0 MJ/kg

[z] Abbreviations Prob = Probability, SE = Standard error, Spec = Species. Based on eight white-tailed deer, five bison , and five wapiti.

[a - b] Means in the same column not followed by the same superscript differ significantly ($P < 0.05$).

3.4 Discussion

3.4.1 *Ad libitum* intakes

Body weight scaled to $kg^{0.75}$, known as the metabolic weight, is the interspecies mean of fasting metabolism for mature mammals (Hudson and Christopherson 1985). It is a useful comparative unit for measuring intake and metabolic rate across species.

No experiments were found in the literature in which DMI of these species were compared when fed a similar diet. The DMI of bison of 111 g $kg^{-0.75}$ while group feeding, and 70 g $kg^{-0.75}$ during individual feeding in the digestibility periods, are lower than values of 134 and 129 g $kg^{-0.75}$ determined in summer/autumn and winter, respectively, for bison eating a 50/50 concentrate/roughage diet (Stanton et al. 1994). Part of the difference between the intakes between studies could be attributed to the fact that the animals used in the study by Stanton et al. (1994) were bulls and the animals used in the present study were female. Although no comparative female vs. male intakes with bison are available, higher intakes have been measured in red deer stags over hinds (Suttie et al. 1987).

The voluntary intakes of 86 g $kg^{-0.75}$ by wapiti fed in groups and 78-90 g $kg^{-0.75}$ when fed individually from this study are higher than the Feb intake of 52 g $kg^{-0.75}$ observed by Jiang and Hudson (1992). Although the animals in the study by Jiang and Hudson (1992) were all female and were fed a similar alfalfa pellet diet, they were, on average, larger animals than those in the current experiment.

The white-tailed deer had the lowest intake (46 g $kg^{-0.75}$) during the group DMI measurement. This could partially be because the pair of deer which were

excluded from the digestibility measurements due to low intakes were included in these measurements. The higher intake for the deer noted during the calorimetry measurements (68 - 93 g $kg^{-0.75}$) may be related to behavioral differences in response to housing and experimental conditions between the species since deer prefer a secluded area. No literature intakes of white-tailed deer fed alfalfa pellets were found, however Holter et al. (1977) fed male and female white-tailed deer fawns a cornmeal based pellet for 15 consecutive months and measured DMI of 58 g $kg^{-0.75}$ during Feb and March, which is 10-49% higher than the Feb-March intake for deer in this study (39-53 g $kg^{-0.75}$). The DMI of 45 g $kg^{-0.75}$ in deer fed a cornmeal-oat mill feed observed by Thompson et al. (1973) in the month of January is closer to the intake in the present study; the deer in both of the other studies were similar weights and ages to the animals in the present study, however, females as well as males were included which could influence mean intakes. The intake for May in our study of 85 g $kg^{-0.75}$ during the digestibility period is 44% higher than the 59 g $kg^{-0.75}$ measured in May by Thompson et al. (1973), and 16% higher than the May DMI of 73 g $kg^{-0.75}$ observed by Holter et al. (1977).

The significant increase in voluntary intake observed in the May-June period has previously been seen in bison, wapiti and white-tailed deer. In a 266 day trial with bison fed varying proportions of concentrate (corn, soybean meal) and roughage (oat hay), there was a substantial reduction in feed intake during the winter in a study by Stanton et al (1994). Intake from d 0 to d 169 (June to Nov.) averaged 8.18 kg d^{-1} compared to the intake of 7.19 kg DM from d 170 to 266 (Nov-March). Hudson et al. (1992) found that wapiti doubled their intakes in spring and summer in comparison

with winter and Suttie et al. (1987) also showed a strong seasonal effect of voluntary intake in red deer hinds in New Zealand, with the highest intakes occurring in the summer months. Intakes have also been found to be highest in spring for white-tailed deer; Short et al. (1969) demonstrated that 2-yr-old white-tailed deer in the southern USA increased their intake from a low in Nov and Dec to a high in spring.

In summary, although long-term group feeding results were not obtained, voluntary intakes observed for all three species in this study were similar to literature values. Behavioral differences between species and an abnormal response of the deer to the pelleted alfalfa diet, however, makes it difficult to use these results to predict intake responses under natural conditions. Our data, however, does support previous findings that native ruminants have lower DMI in winter months than in spring months.

3.4.2 Digestibility and urinary output

No previous study has compared digestibility of a diet by these three species. The observation of no digestibility differences between these three species in any dietary component (Table 3.2), particularly in the fibrous parts of the feed, was unexpected. The results of the research into passage rates through the digestive tracts of the three species in this study will perhaps help further explain the unexpectedly low fiber digestion found in the bison and wapiti.

No previously published values for bison DM digestibility of alfalfa pellets were found. Bison fed alfalfa hay exhibited apparent DM digestibilities of 77.5% (Richmond et al.1976) and 70.1% (Koch et al.1995), respectively. The fact that the feed in this study was in pelleted form may have influenced apparent digestibility in

bison since pellets pass through the digestive tract more quickly than feeds with long particle sizes which may also have reduced fiber digestion (Hironaka et al. 1996). It was expected that bison would digest the fibrous parts of the feed most completely since they are roughage-grass eaters whereas wapiti and deer are intermediate and browse feeders respectively (Hofmann 1989). In a study comparing bison to yak and cattle, it was found that bison had the highest digestibility's of NDF and ADF when fed either grass or alfalfa hay (Richmond et al. 1976). One explanation for the ability of bison to digest forages more than cattle suggested by Hawley et al. (1981) is that they have an enhanced capacity to recycle nitrogen to their rumen. This would reduce the ruminal energy:nitrogen ratio and the microbial competition for nitrogen, and thus reduce the depression of cellulolysis. However, since the alfalfa contained 13.9 % crude protein, ruminal availability of N should not have been limiting in this experiment.

Wapiti hinds fed alfalfa pellets in our study had a DM digestibility of 51.2% from Feb-May which is very similar to that observed for suncured pelleted alfalfa in August (48%) by Hudson (1993) and of 46.5% in Red Deer fed lucerne hay in winter in New Zealand (Suttie et al. 1987). In the latter study, red deer were found to have a 34% higher DM digestibility in the summer than in the winter. In contrast, digestibility of DM was numerically 9% lower in May than in March in our study. Westra and Hudson (1981) found no temperature effect on digestive function in wapiti. A significant difference may have been observed in our experiment if the study was further into the summer season. Wapiti were found to have NDF and ADF digestibilities of 44.0% and 41.3%, respectively, which are lower than previously

published values of 50.6% and 49.8% for wapiti consuming alfalfa hay (Mould and Robbins 1982). Again, the form of feed in this study could lend an explanation for the lower apparent digestibility of fiber.

No literature value for DM digestibility of alfalfa pellets in white-tailed deer was found however, deer fed alfalfa hay had an apparent DM digestibility of 55.2% during a feeding trial in an undisclosed time of year (Robbins et al. 1975). This is higher than the average of 46.9% obtained in our trial. The NDF and ADF digestibilities for white-tailed deer of 37.2 % and 32.7 % respectively are similar to the values found by Mould and Robbins (1982) of 39 % and 35 % respectively for white-tailed deer fed alfalfa hay. This perhaps suggests that white-tailed deer are not as sensitive to feed form as bison and wapiti. With expected higher passage rates through the digestive system in concentrate selectors (Hofmann 1988), pelleting may not have as great an effect on DM digestibility as with the other two species.

Bison were found to have a nitrogen balance of 27.1 g d^{-1}. No literature values were found for comparison. The value of 27.3 g d^{-1} found for wapiti in this study is higher than a previously published value for red deer of 14.8 g d^{-1} at a high level of feeding at an ambient temperature of 16°C (Simpson et al. 1978). The overall mean of nitrogen retention of -0.3 g d^{-1} in white-tailed deer is lower than, but not far from, a previously published value of 1.5 g d^{-1} (Hoter et al. 1979). The May- June N retention in this study (3.7 g d^{-1}) was also close to the summer value found by Holter et al. (1979) of 5.0 g d^{-1}. The animals in the study by Holter et al. (1979) were also fed a pelleted diet ad libitum. The negative nitrogen balance in the deer in winter in this study indicate that the feed consumed was not providing adequate amounts of

nitrogen or energy, and could be related to a greater stress in the March period. The deer had the most hair contamination in the feces and urine samples; such contamination may have slightly reduced their calculated nitrogen balance.

3.4.3 Methane Production

3.4.3.1 Effect of species on methane production

Bison had the greatest percentage of gross energy intake (GEI) lost as methane between the three species at 6.6% when averaged over both seasons (Table 3.3). Bison methane production was 8.6% of GEI in March - April compared with 4.7% in May. The DMI of the bison in the March - April period was only 65% of that observed in the May June period. This would have created a longer retention time of feed in the March-April period which would have enhanced the activity of methanogenic bacteria in the rumen. Increasing passage rates by 63% through the digestive tract has been shown to lower methane production by 29% in cattle fed identical diets (Okine et al. 1989). The higher percentage of GEI lost as methane by bison in comparison with wapiti and deer was expected since bison are classified as roughage/grass eaters by Hofmann (1989) and have been shown to consistently select lower quality forages then cattle (Towne et al. 1988). Such feed would move through the digestive system slower and be conducive to greater methane production. There are no experiments in the literature in which methane production of bison have been measured but the results of this study suggest that bison lose a similar proportion of their GEI as methane as cattle, which were found to lose 5-7% of their ingested GEI when fed pelleted alfalfa (Hironaka 1996).

Averaged over both measurement periods, the percentage of GE lost as methane by wapiti was 5.2% of GEI and which was lower ($p<0.05$) than the bison but higher than deer productions. Again, the amount of methane produced relative to the other species was expected since wapiti are classified as intermediate feeder by Hofmann (1988). No literature values for methane production in wapiti was found. Sika deer (*Cervus nippon*), which are also classified as intermediate feeders by Hofmann (1988), were found to lose 6.6% of their GEI as methane when fed an unspecified diet (Zhonokuan et al. 1996). Numerically wapiti produced more methane, as a percentage of GEI, in March -April than in May -June but this difference was not significant.

White-tailed deer, which have been classified as concentrate selectors (Hofmann 1989), had a lower ($P <0.05$) methane production than either bison or wapiti. The amount of methane lost by deer expressed as a percentage of GEI in the March - April, and May - June periods of 3.5 and 3.1% respectively (Table 3.3), compares to literature values where it has been found that white-tailed deer consuming a variety of diets over two different years from May to Oct produced a range of methane from 3.5% to 4.7% of GEI (Holter et al. 1979).

3.4.3.2 *Effect of temperature on methane production*

Traditionally it has been thought that methane production in ruminants is lowest in the cold weather (Kennedy et al. 1978; Christopherson and Kennedy 1983). However in this study, although the actual amount of methane released from each animal in L d^{-1} was not significantly different between periods, the proportion of GEI lost as methane was 59% higher in Feb-March than April-May (Table 3.3). There was

a difference with all three species but the greatest difference occurred with bison, GEI lost as methane in the first period (winter) for bison was 8.6% versus the second period of 4.7%. This is contrary to earlier studies where it has been suggested that methane production in cattle decreased with cold temperature (Christopherson and Kennedy 1983), but consistent with later studies. Von Keyserlingk (1993) in sheep found 20% more methane was produced at 4.7°C than at 21 °C when feed intakes were similar. Similarly, Dymtruk et al. (1995) measured 19% more methane production in cattle at -23°C than at 29°C.

The lower production in April May could have been at least partly due to higher intake since Dymtruk et al. (1995) found that the proportion of GEI lost as methane decrease with increased intakes. During calorimetry measurements DMI in Feb-March were 82, 81, and 72% of that measured in bison, wapiti, and deer, respectively in April-May (Table 3.1). Corresponding methane production as a proportion of GEI were 183, 160, and 113% higher in March. These large differences in methane production therefore appear to be more than can be attributed to intake differences.

3.4.3.3 *Global estimates of methane produced from game farms*

From the above information it can be concluded that using a figure of 9% of GE lost as methane, as has been done in the past (Crutzen et al 1986), for the calculation of global contribution of methane release from wild ruminants, would likely lead to an overestimate, particularly with wapiti and white-tailed deer. The results from this study would suggest that 6.6, 5.2, and 3.3% of GEI lost as methane would be more accurate numbers to use for bison, wapiti, and white-tailed deer

respectively on Canadian game farms. With the estimated numbers of animals on game farms in 1995 in Canada of 19144 wapiti, 7039 white-tailed deer, and approximately 56000 bison, (Houdepohl 1997); and using the calculated daily methane output per day from this study of 121, 87, and 32 CH_4 L d^{-1} for bison, wapiti, and white-tailed deer respectively, the annual contribution of each species to global methane production in can be calculated. It must be remembered however, that such an estimate is a minimum estimate of the contribution of Canadian farmed native ruminants since the animals in our trials were sub adults and all females with average weights of 196, 151 kg, and 34 kg for bison, wapiti, and deer respectively (Table 3.1). In addition, less methane is likely be produced when a pelleted diet such as that used in this study is fed. Nevertheless the values from this study, are 1766, 434, and 61 tonnes yr^{-1} of methane for bison wapiti, and white-tailed deer respectively. When these values are used against the overall contribution of methane contributed to the atmosphere, (602 Tg); an average from Khalil and Rasmussen 1987; Bingmer and Crutzen 1987; Ciceron and Oremla 1988; IPCC 1990; Fung et al.1990; Watson et al. 1992) 2.9×10^{-3} %, 7.2×10^{-5} %, and 1.0×10^{-5} % of the global release of methane to the atmosphere would originate from wapiti, white-tailed deer, and bison on Canadian game farms. Collectively, the contribution of Canadian game farmed bison, wapiti, and white-tailed deer to the global release into the atmosphere is not less than 0.002 Tg yr^{-1} or 3.8×10^{-4} % of total world products.

3.4.4 Metabolizable energy intake

The intake of ME averaged over both calorimetry measurement periods for bison from this study was 514 kJ $kg^{-.75}$ which is the lowest between the three species. No values for ad libitum MEI were found in the literature for bison.

The voluntary intake of ME for wapiti was 438 and 943 kJ $kg^{-0.75}$ in Feb and May respectively (Table 3.3). The Feb intake is below the mean ME_m requirement for wapiti in winter from literature where it was found that an average voluntary MEI for winter was 550 kJ $kg^{-0.75}d^{-1}$ (from Jiang and Hudson 1994; Jiang and Hudson 1992; Fennessy et al. 1981; Cool 1992). A seasonal effect on calculated MEI was also found in red deer (*Cervus elaphus*) by Suttie et al. (1987), with MEI of 500 kJ $kg^{-0.75}$ in summer and 400 kJ $kg^{-0.75}$ in winter. This seasonality would be expected with the spring summer period typically being a time of rapid growth for the animal.

The voluntary MEI obtained for white-tailed deer from this study in March was 558 kJ $kg^{-0.75}$, which is slightly higher than previously published voluntary intakes of 548 kJ $kg^{-0.75}$, 322-448 kJ $kg^{-0.75}$, and 523 kJ $kg^{-0.75}$ from Ullrey et al. (1970), Worden and Pekins (1995), and Thompson et al. (1973) respectively. The MEI in May in the present study for white-tailed deer was 1008 kJ $kg^{-0.75}$ which is higher than the average summer MEI found in the literature of 740 kJ $kg^{-0.75}$ from Thompson et al. (1973) and Holter et al. (1977). As seen from the above discussion there is considerable variability seen in *ad lib* MEI and more data needs to be gathered under normal farming situations.

3.4.5 Heat production and estimated maintenance requirements

The HP for the three species in this study combined over both measurement periods was 652 kJ $kg^{-0.75}$ d^{-1}, 698 kJ $kg^{-0.75}$ d^{-1}, and 884 kJ $kg^{-0.75}$ d^{-1} for bison, wapiti, and white-tailed deer respectively (Table 3.3).

When an animal is below its lower critical temperature it is required to expend extra energy to keep warm. During both measurement periods, most of the experimental animals would have been above their lower critical temperatures. Bison have been reported to have lower critical temperatures, in still air when fed 100g feed per unit metabolic weight per day, of below -30°C (Christopherson et al. 1979). The lower critical temperature for wapiti in the winter fed *ad libitum* alfalfa hay and pellets was -20°C in a study of Parker et al. (1984). White-tailed deer have been found to have much higher lower critical temperatures in the winter of around -2°C (Mautz et al.1992). The higher calculated maintenance requirement found for deer discussed below could reflect this high lower critical temperature in that the deer may have been below their critical temperature, since mean environmental temperature was only 0.6°C during the first period, which would require more energy at maintenance to maintain body heat.

Stress associated with being put into the chambers may have increased heat production however, this was not considered to be a major source of error. All animals were well adjusted to the chambers, particularly by the second measurement period since a 5-d fecal and urine collection period preceded each respiration measurement. Calorimetry measurement periods of longer than 1/d, which would

have aided adaptation to crates, were not possible because of animal welfare considerations.

Table 3.3 shows the calculated ME_m for the animals. In March all but two animals had HP > MEI, indicating that these animals had ME intakes below maintenance. In the second period (May 1995), 8 of 12 animals had MEI > HP, indicating that their MEI was above maintenance. Estimated efficiencies of ME use for maintenance and gain were used in the calculation of ME requirements for maintenance. Using such estimates could have a significant effect on estimated maintenance requirements only when MEI was substantially different from HP. Further, if efficiency of use of ME is less for gain than maintenance, then using incorrect efficiency estimates would be expected to result in greater errors when animals were fed above maintenance. Some of the deer, in particular, ate above maintenance and some ate below maintenance which resulted in a large spread in the calculated values for maintenance. Any time the animals were eating below maintenance, values calculated for maintenance using either the cattle or wapiti efficiencies did not differ substantially since the efficiency of ME use for maintenance for cattle and wapiti were so similar (i.e. 63%). However when MEI intakes were greater than HP using a value of 38.5% for the efficiency of ME use for gain, which is the cattle value (NRC 1984), resulted in very low and even negative estimates of ME required for maintenance for white-tailed deer. This was taken to indicate that the efficiency of ME use for gain was too low, suggesting that deer utilize ME with a greater efficiency than do beef cattle. It must be recognized, however, that the Agricultural Research Council (1980) indicates that the ME of pelleted diets is used

with a greater efficiency for gain than the ME from non-pelleted diets. Although both ways of estimating ME_m are given in Table 3.3, in the following discussions only ME_m calculated from wapiti K_g will be used.

The average calculated ME_m value for maintenance for bison in March was 706 kJ $kg^{-0.75}$ d^{-1} and for May was 763 kJ $kg^{-0.75}$ d^{-1}. The May value in particular is considered to be a good estimate of ME_m since the estimated value was very close to MEI. No previously published values for ME requirement for maintenance in bison was found. The comparative value for cattle, with no adjustment for season, is 611 kJ $kg^{-0.75}$ (NRC 1984), which is 14-20% lower than the values for bison. This difference, however, is within experimental error and at least some of it might be expected due to a greater effect of stress in the bison measurement than in similar cattle measurements.

This study showed an average calculated ME_m value for maintenance for wapiti of 683, and 733 kJ $kg^{-0.75}$ d^{-1} in May and March respectively. These estimates are also somewhat higher than maintenance requirements cattle (NRC 1984). The March value in this study is also somewhat higher than both the winter value determined by Jiang and Hudson (1994) of 493 kJ $kg^{-0.75}$ d^{-1}, and the value determined by both Fennessy et al. 1981, and Cool (1992) of 570 kJ $kg^{-0.75}$ d^{-1}. However, HP was 35% greater than MEI which means the accuracy of the estimate is somewhat reduced. The animals in the study by Fennessy et al. (1981) were stags and the animals in the study by Cool (1992) were calves, which would, if anything, be expected to have an increased requirement. Calculated ME_m for wapiti in spring (May) was similar to the value of 728 kJ $kg^{-0.75}$ d^{-1} published by Jiang and Hudson

(1994), but lower than values published for wapiti in the summer of 936 kJ $kg^{-0.75}$ d^{-1}, and 878 kJ $kg^{-0.75}$ d^{-1} (Jiang and Hudson 1992, and Wairimu et al. 1992 respectively). An explanation for the difference in the ME_m found in the present study and those of Jiang and Hudson (1992) is that their values include the energy cost of free ranging on a pasture. It has been estimated that ecological maintenance (energy for energy equilibrium of free existence) is about 1.6 times physiological maintenance (Jiang and Hudson 1992).

The white-tailed deer calculated March ME_m value in the present study was 560 kJ $kg^{-0.75}$ d^{-1}, which is similar to values determined by Ullrey et al. (1970) of 548 kJ $kg^{-0.75}$ d^{-1}, Thompson et al. (1973) of 523 kJ $kg^{-0.75}$ d^{-1}, and higher than the range determined by Worden and Pekins of 322 - 448 kJ $kg^{-0.75}$ d^{-1} (1995).

The May calculated ME_m for white-tailed deer of 1176 kJ $kg^{-0.75}$ is higher than the summer values determined by Holter et al. (1977) or Thompson et al. (1973) of 678, and 803 kJ $kg^{-0.75}$ respectively. It is however apparent that the estimated maintenance requirement would have been reduced if a lower efficiency of ME use for gain, such as with cattle was used thus not much reliance can be placed on this value.

In summary, the estimates of ME required for maintenance for all three species for this experiment using the wapiti efficiency of gain (k_g = 67%) is 706, 683, and 560 kJ $kg^{-0.75}$ for bison, wapiti and deer respectively in the winter. In spring months, only the bison (763 kJ $kg^{-0.75}$) and wapiti (733 kJ $kg^{-0.75}$) estimated values for ME_m from this experiment are considered to be reliable enough for use.

3.4.6 DE and ME content of diet

Dietary DE and ME contents are given in Table 3.4. The DE content of alfalfa pellets for bison and wapiti in this study (9.2 MJ kg^{-1}) is lower than the average content for alfalfa hay of 11.1 MJ kg^{-1}, reported in the beef cattle NRC (1996). Similarly, the DE content of the diet in deer was only 82% of the NRC (1996) values (7.2 vs. 8.3 MJ kg^{-1}). Also, the ME content of the pelleted diet in this experiment was only 87-95% of ME content of alfalfa hay in NRC (1996). Pelleting of the diet, however, reduces dietary DE and ME content (Hironaka et al. 1996).

In this study ratios of DE to ME were 0.79, 0.85, and 0.85 for bison, wapiti, and deer respectively. This compares to the common value used for beef cattle of 0.82 (NRC 1996). The lower ratio of ME to DE in bison was because they produced more methane during winter (8.6% of GE; Table 3.3). The wapiti ratio of ME to DE of 0.85 is slightly higher than the value used in the 1996 NRC nutrient requirements for beef cattle. For deer, the ME:DE ratio of 0.88 observed in May was identical to that determined by Holter et al. (1977), and was also very close to the value of 0.87 found by Thompson et al. (1973) with deer. The animals in both of these studies were fed a corn-meal based diet.

3.4.7 Conclusions

Pelleted alfalfa as a sole dietary source was fine for the wapiti and bison, but not for deer.

The DMI of the animals in the present study was similar to previously published values and support findings that bison, wapiti, and white-tailed deer have

greater DMI in spring months than in winter months. Voluntary MEI averaged over both periods was 514, 691, and 783 kJ $kg^{-0.75}$ for bison, wapiti, and white-tailed deer respectively, with value for bison being the only value ever measured for the species. Surprisingly, however, the three species did not differ in their ability to digest dry matter, organic matter, energy, nitrogen, NDF, or ADF of the pelleted alfalfa diet.

It can be concluded that bison lose the greatest proportion of their gross energy intake as methane followed by wapiti and then white-tailed deer with all three species producing more methane per unit of food consumed in March than during May.

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4. General discussion and conclusions

4.1 Acceptance of the Diet

Alfalfa is a commonly fed forage on game farms and was therefore thought to be a good representative feed to use to simulate a game farm situation. It performed well as a sole dietary source for the bison and wapiti, however there were signs that the deer needed browse material to supplement the diet since they were observed chewing on each other's hair with resulting hair loss. This could have been a nervous response but is more likely a response to not having browse material to chew on since it occurred both in the group pens as well as in the digestibility crates. The natural diet of white-tailed deer includes several different types of browse including balsam popular, bearberry, juniper, rose, willow, alfalfa, aster and blue bells (Stelfox 1993). Future work is needed to identify diets which will maintain deer in healthy states on game farms.

4.2 Limitations of this experiment

The mean recoveries of nitrogen released into the bison/wapiti chamber was 60% (SD= 4.6, n= 5). The comparable figure for the deer chamber was 58% (n=1). We are concerned about these low recoveries since the 60% recovery factor was used to adjust HP, methane production, and oxygen consumption. We attempted to find the reason(s) for the low recovery but have only been partially successful. We did identify a design flaw in the calorimetry system in that air temperature and pressure were measured at a considerable distance after the air had passed through the orifice plate

flow meter. These measurements should have taken place just before the meter. We estimated that the pressure of the air was underestimated by approximately 30 mmHg. We have no good estimate of the effect of measurement site on air temperature. We thus estimate that these design flaws could have accounted for 10 of the 40% error in measurement (i.e. the recovery factor would have been 70% in a properly designed system). We have been unable to account for the remaining source of error but have assumed that it resides with the flow measurements since measurements of expired air oxygen relative to methane concentrations appeared to be approximately correct. This would rule out the possibility of low recoveries of nitrogen being due to a low decrement in oxygen passing through the system. Although both chambers showed some degree of negative pressure through the use of a manometer, at times the larger chamber used for the bison and wapiti showed only a very small degree of negative pressure. This could indicate that there was air escaping from the chamber. One likely place for this to have occurred was at the back door of the chamber which was a very large piece of plywood fastened to the chamber with clamps. Although not considered to be a major source of error, it is recommended that new crates be constructed for similar projects. However, the possibility of leaks from the chambers as being the cause of low recoveries is not great because the percentage recovery of nitrogen released in the tightly sealed deer chamber was similar to that in the bison/wapiti chamber. Unfortunately, then, we cannot fully explain the lack of recovery of 30% of the released nitrogen in the system. We recommend that in future a rotometer be used routinely to check results from the electronic flow meter (we did use a rotometer but it

was too large for the system and pressure and temperature readings were not taken to allow correction of rotometer flow to standard temperature and pressure).

Obviously, numbers of experimental animals affected what was found to be significant and what wasn't. Using only five bison, five wapiti, and four pairs of deer limited the findings of this experiment.

For better accuracy in a comparative study such as the present study, it would be ideal to have animals that are all similarly accustomed to human handling. Although the deer were bottle raised as fawns, they were equally as skittish as the bison which had not been handled much before the experiment. Also, for an accurate value of the global contribution of methane from farmed bison, wapiti, and white-tailed deer, an experimental group consisting of both animals of different sizes could have been used.

Experimentation dates during more extreme months of the seasons would have likely resulted in a more distinct seasonal effects in digestibility, intake, and methane production in each species.

The problem of having to rely on generators for electricity was evident during the calorimetry measurement period with one of the bison, when the generator quit working for a short time, which resulted in loss of numbers for methane production upon restoration of the power. Researchers now looking to the Ministik research station will no longer have this problem since a power line has been run to the facility.

4.3 Future research

We have commenced analysis of Co-EDTA and chromium in fecal samples of bison, wapiti, and white-tailed deer which, when analysis is complete, will add a new

dimension to our understanding of the digestive characteristics of these species and will enable the effect of passage rate on methane production in these animals to be examined.

More research is needed examining digestibility, nutrient requirements, and intake between these three species so comparative efficiencies under different feeding and management systems can be assessed.

As game farms increase in number, more research into digestive physiology and nutrition will be very valuable for the industry to have to capitalize on species specific traits which enable them to be efficient, and to survive in the wild.

A less invasive technique for the measurement of methane production over a 24hr period is the SF_6 tracer technique (Johnson et al. 1994). This technique could be useful for obtaining methane production in grazing animals, over longer periods of time under less stressful conditions. This would be useful for the determination of methane loss into the atmosphere by animals in the wild under natural environments consuming natural diets.

4.4 Implications

The hypothesis tested in this theses was that the proportion of feed energy lost as methane differs between species, and that methane and heat production is seasonal. Seasonality in both heat production and methane production was supported by the results of this experiment when considering all three of the test species combined. Species differences combined over both measurement periods only occurred in methane production, and not in heat production, with bison losing the greatest

proportion of gross energy intake to methane followed by wapiti and then white-tailed deer. The results of this thesis supports recent findings that methane production is higher at colder temperatures in ruminants but the biological reason for this is unknown.

The amount of methane produced by wild ruminants in Canada is very insignificant to the global release of methane, and even more insignificant to the overall emission of all greenhouse gases. Strategies regarding the reduction of greenhouse gas emissions would be better directed towards the release of CO_2 into the atmosphere by the burning of fossil fuels in the world and the CH_4 emission from use of non-renewable resources.

4.5 Literature Cited

Johnson, K. A., Huyler, M. T., Westberg, H. H., Lamb, B. K. and Zimmerman, P. 1994. Measurement of methane emissions from ruminant livestock using a SF_6 tracer technique. Environ. Sci. and Technol. 28: 359.

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5. Appendices- Raw data

In the following pages, seasons 1 and 2 are the February, March and April, May periods respectively. The number "2" in front of an animal's ear tag number indicates the animal in the April May period. In the digestibility trial, deer pair 4,12 were not included in the analysis because of very low dry matter intake. In the calorimetry trials, bison 45 was excluded from analysis in both the winter and spring trial because of a problem with the methane analyzer in period one and a power failure in period two, resulting in unrealistic values for methane production. 2Bison 06 was also excluded from the calorimetry calculations due to excessively low DMI.

For the following pages: week 1 refers to 03/06/95 - 03/11/95, week 2 = 03/13/95 - 03/18/95, week 3 = 03/20/95 - 03/25/95, week 4 = 05/01/95 - 05/06/95, week 5 = 05/15/95 - 05/20/95, and week 6 = 05/22/95 - 05/27/95.

The weight used in the calorimetry calculations for Deer 1,2 during period 1 was 32.8 kg (it is not listed in the following pages).

				Temp °C		
Animal	Weight (kg)	$Wt^{0.75}$	Week#[1]	Max	Min	Mean
Bison01	162.2	45.45	2	6.6	-3.7	1.45
Bison03	167.9	46.64	1	-9.8	-23.7	-16.75
Bison06	197.6	52.70	3	7.2	-4	1.6
Bison08	181.1	49.37	1	-9.8	-23.7	-16.75
Bison45	177.95	48.72	3	7.2	-4	1.6
Elk02	152.6	43.42	3	7.2	-4	1.6
Elk03	155	43.93	2	6.6	-3.7	1.45
Elk05	146.8	42.17	1	-9.8	-23.7	-16.75
Elk14	138.9	40.46	3	7.2	-4	1.6
Elk27	152.2	43.33	2	6.6	-3.7	1.45
Deer4,12	28.8	12.43	1	-9.8	-23.7	-16.75
Deer5,15	38.7	15.52	1	-9.8	-23.7	-16.75
Deer11,14	34.15	14.13	3	7.2	-4	1.6
2Bison01	195.7	52.32	5	19.3	1.9	10.6
2Bison03	218.3	56.79	4	14.8	-0.5	7.15
2Bison06	222.4	57.59	5	19.3	1.9	10.6
2Bison08	233.4	59.71	4	14.8	-0.5	7.15
2Bison45	200.15	53.21	6	18.3	0.7	9.5
2Elk02	169.5	46.98	6	18.3	0.7	9.5
2Elk03	159.6	44.90	5	19.3	1.9	10.6
2Elk05	161.4	45.28	4	14.8	-0.5	7.15
2Elk14	153.8	43.67	6	18.3	0.7	9.5
2Elk27	122.8	36.89	5	19.3	1.9	10.6
2Deer1,2	31.55	13.31	5	19.3	1.9	10.6
2Deer4,12	30	12.82	4	14.8	-0.5	7.15
2Deer5,15	41.25	16.28	4	14.8	-0.5	7.15
2Deer11,14	36.35	14.80	6	18.3	0.7	9.5
Bison	**177.35**	**48.58**		**0.28**	**-11.82**	**-5.77**
Elk	**149.1**	**42.66**		**3.56**	**-7.82**	**-2.13**
Deer	**33.9**	**14.02**		**-4.13**	**-17.13**	**-10.63**
2Bison	**212.4**	**55.93**		**17.30**	**0.70**	**9.00**
2Elk	**153.4**	**43.54**		**18.00**	**0.94**	**9.47**
2Deer	**34.8**	**14.30**		**16.80**	**0.40**	**8.60**

Nutrient intake during digestibility trial						
Animal	**DMI kg/d**	**DMIg/kg/d**	**DMIg/kg$^{0.75}$/d**	**E (kJ/d)**	**N (g/d)**	**Ash (g/d)**
Bison01	2.14	13.21	47.13	38582.0	47	177
Bison03	1.86	11.08	39.88	33502.5	41	154
Bison06	1.86	9.40	35.25	33466.5	41	154
Bison08	3.33	18.41	67.53	60052.4	73	276
Bison45	3.85	21.66	79.10	69418.7	85	319
Elk02	2.43	15.90	55.88	43697.4	53	201
Elk03	2.73	17.60	62.10	49137.1	60	226
Elk05	1.91	13.04	45.38	34475.2	42	159
Elk14	1.66	11.92	40.93	29828.1	36	137
Elk27	3.20	21.04	73.89	57674.8	71	265
Deer4,12	0.45	15.45	35.79	8015.4	10	37
Deer5,15	0.73	18.89	47.11	13166.9	16	61
Deer11,14	1.06	31.07	75.11	19110.9	23	88
2Bison01	4.54	23.19	86.73	82227.6	102	378
2Bison03	5.50	25.19	96.81	99622.6	124	459
2Bison06	4.23	19.03	73.48	76682.9	95	353
2Bison08	5.63	24.10	94.22	101941.9	127	469
2Bison45	3.67	18.34	68.97	66499.6	83	306
2Elk02	5.66	33.37	120.40	102485.5	128	472
2Elk03	5.67	35.50	126.18	102666.7	128	473
2Elk05	4.36	27.03	96.33	79038.5	98	364
2Elk14	5.63	36.63	129.00	102086.9	127	470
2Elk27	4.95	40.29	134.13	89656.7	112	413
2Deer1,2	1.04	32.93	78.05	18826.5	23	87
2Deer4,12	0.97	32.47	75.98	17648.7	22	81
2Deer5,15	1.40	33.89	85.89	25331.5	32	117
2Deer11,14	1.53	42.15	103.49	27759.5	35	128
Bison	**2.61**	**14.75**	**53.78**	**47004.43**	**57.47**	**216.17**
Elk	**2.39**	**15.90**	**55.64**	**42962.51**	**52.53**	**197.58**
Deer	**0.75**	**21.80**	**52.67**	**13431.04**	**16.42**	**61.77**
2Bison	**4.71**	**21.97**	**84.04**	**85394.94**	**106.24**	**393.02**
2Elk	**5.25**	**34.56**	**121.21**	**95186.87**	**118.42**	**438.09**
2Deer	**1.24**	**35.36**	**85.85**	**22391.53**	**27.86**	**103.05**

Nutrient intake during dig trial----------

Animal	OMI (g/d)	Lignin (g/d)	NDF (g/d)	ADF(g/d)
Bison01	1965	234	1272	932
Bison03	1706	203	1105	810
Bison06	1704	203	1103	809
Bison08	3058	364	1980	1451
Bison45	3535	421	2289	1677
Elk02	2225	265	1441	1056
Elk03	2502	298	1620	1187
Elk05	1755	209	1137	833
Elk14	1519	181	983	721
Elk27	2937	350	1901	1394
Deer4,12	408	49	264	194
Deer5,15	670	80	434	318
Deer11,14	973	116	630	462
2Bison01	4160	508	2677	1970
2Bison03	5039	615	3243	2386
2Bison06	3879	473	2496	1837
2Bison08	5157	629	3319	2442
2Bison45	3364	410	2165	1593
2Elk02	5184	633	3336	2455
2Elk03	5193	634	3342	2459
2Elk05	3998	488	2573	1893
2Elk14	5164	630	3323	2445
2Elk27	4535	553	2919	2148
2Deer1,2	952	116	613	451
2Deer4,12	893	109	575	423
2Deer5,15	1281	156	825	607
2Deer11,14	1404	171	904	665
Bison	**2393.43**	**285.14**	**1549.65**	**1135.77**
Elk	**2187.62**	**260.63**	**1416.39**	**1038.11**
Deer	**683.90**	**81.48**	**442.80**	**324.53**
2Bison	**4319.78**	**527.08**	**2779.96**	**2045.50**
2Elk	**4815.11**	**587.52**	**3098.72**	**2280.05**
2Deer	**1132.70**	**138.21**	**728.94**	**536.35**

Digestibility Trial Fecal Output Analysis———

Animal	DM kg/d	% DM	E kcal/kg	E kJ/kg	E kJ/d	Protein %	N (g/d)
Bison01	1.05	94.72	4199.5	17570.5	18484.2	12.4	21
Bison03	0.98	94.86	4337.8	18149.4	17804.5	9.9	16
Bison06	1.11	95.35	3846.2	16092.3	17907.5	13.3	24
Bison08	1.30	95.17	4338.1	18150.4	23548.3	10.8	22
Bison45	2.07	95.44	4102.5	17164.9	35517.5	11.5	38
Elk02	1.23	95.32	4033.1	16874.3	20735.1	15.1	30
Elk03	1.32	95.43	4354.2	18218.0	24069.6	12.7	27
Elk05	0.84	95.32	4391.7	18374.7	15364.9	12.5	17
Elk14	0.71	95.36	4291.0	17953.5	12664.4	12.6	14
Elk27	1.51	95.52	4320.0	18074.9	27343.7	12.2	29
Deer4,12	0.28	95.44	4487.8	18777.0	5170.2	11.7	5
Deer5,15	0.35	95.45	4428.6	18529.3	6569.5	10.8	6
Deer11,14	0.56	95.10	4318.9	18070.1	10157.2	10.9	10
2Bison01	2.08	94.31	4122.8	17249.8	35886.5	11.3	38
2Bison03	2.99	94.94	4308.3	18025.9	53832.6	10.6	50
2Bison06	2.30	94.73	4042.8	16915.1	38897.9	10.5	39
2Bison08	2.88	94.89	4180.3	17490.4	50386.3	10.8	50
2Bison45	1.87	95.15	4025.6	16842.9	31523.2	11.1	33
2Elk02	2.95	95.30	4395.9	18392.2	54345.4	11.1	52
2Elk03	3.01	95.21	4271.7	17872.8	53768.5	11.6	56
2Elk05	1.97	95.35	4410.9	18455.0	36363.7	12.2	38
2Elk14	2.93	95.04	4539.4	18992.8	55709.8	11.7	55
2Elk27	2.60	95.66	4241.4	17746.0	46104.2	12.5	52
2Deer1,2	0.53	95.20	4169.2	17443.9	9323.8	11.8	10
2Deer4,12	0.51	95.96	4465.3	18682.6	9518.8	11.1	9
2Deer5,15	0.72	95.21	4388.9	18363.2	13223.3	10.9	13
2Deer11,14	0.80	95.55	4437.5	18566.5	14944.2	10.8	14
Bison	**1.30**	**95.11**	**4164.79**	**17425.48**	**22652.41**	**11.58**	**24.12**
Elk	**1.12**	**95.39**	**4277.98**	**17899.07**	**20035.54**	**13.01**	**23.38**
Deer	**0.40**	**95.33**	**4411.75**	**18458.76**	**7298.99**	**11.12**	**7.02**
2Bison	**2.42**	**94.80**	**4135.95**	**17304.81**	**42105.29**	**10.85**	**41.93**
2Elk	**2.69**	**95.31**	**4371.84**	**18291.78**	**49258.32**	**11.83**	**50.77**
2Deer	**0.64**	**95.48**	**4365.21**	**18264.05**	**11752.51**	**11.16**	**11.41**

Dig. fecal output analysis

Animal	% Ash	Ash (g/d)	OM (g/d)	Lignin %	Lignin(g/d)	NDF %	NDF (g/d)
Bison01	13.4	141	911	22.1	232	67.7	712
Bison03	13.6	133	848	20.6	202	67.1	658
Bison06	20.9	233	880	26.1	290	67.9	755
Bison08	11.5	149	1148	22.4	290	71.8	931
Bison45	15.0	311	1758	21.3	442	69.8	1444
Elk02	16.7	206	1023	19.8	244	63.3	778
Elk03	13.3	175	1146	18.5	245	67.0	885
Elk05	11.7	98	738	19.6	164	70.4	589
Elk14	13.3	94	612	19.4	137	68.4	482
Elk27	12.4	188	1325	18.1	273	69.0	1043
Deer4,12	11.7	32	243	22.8	63	70.6	194
Deer5,15	10.9	39	316	30.5	108	68.3	242
Deer11,14	11.8	66	496	19.0	107	69.9	393
2Bison01	14.8	307	1773	20.7	431	74.5	1549
2Bison03	13.2	395	2591	20.2	604	71.4	2132
2Bison06	18.8	433	1867	26.4	608	75.2	1729
2Bison08	13.6	391	2490	23.4	674	71.2	2052
2Bison45	17.7	331	1540	23.2	434	69.0	1292
2Elk02	13.6	403	2552	20.8	614	68.7	2030
2Elk03	13.4	402	2606	20.1	606	69.4	2087
2Elk05	13.1	258	1712	18.5	365	69.1	1361
2Elk14	13.6	399	2534	19.5	572	66.3	1944
2Elk27	14.4	374	2224	20.0	520	68.5	1781
2Deer1,2	13.9	74	460	21.2	113	70.8	378
2Deer4,12	11.4	58	451	17.9	91	67.9	346
2Deer5,15	11.4	82	638	18.8	135	70.7	509
2Deer11,14	12.4	100	705	18.0	145	70.3	566
Bison	**14.90**	**193.52**	**1108.96**	**22.49**	**291.23**	**68.83**	**900.01**
Elk	**13.49**	**152.13**	**968.75**	**19.07**	**212.34**	**67.61**	**755.52**
Deer	**11.47**	**45.77**	**351.56**	**24.11**	**92.62**	**69.60**	**276.49**
2Bison	**15.62**	**371.55**	**2052.21**	**22.79**	**550.18**	**72.26**	**1750.71**
2Elk	**13.63**	**367.39**	**2325.57**	**19.80**	**535.53**	**68.39**	**1840.53**
2Deer	**12.29**	**78.67**	**563.58**	**18.96**	**121.10**	**69.94**	**449.93**

	Dig. fecal analysis		Urine Analysis					
Animal	ADF %	ADF (g/d)	% N	E cal/g	kg/d	%DM	E kcal/d	N bal g/d
Bison01	51.1	538	0.32	1979	4.1	0.02	172.2	12.9
Bison03	51.6	506	0.83	2095	2.6	0.03	186.9	3.7
Bison06	53.8	599	1.21	2297	1.7	0.06	219.4	-3.3
Bison08	55.8	724	1.02	2223	3.0	0.05	332.6	20.4
Bison45	54.4	1125	0.70	1952	3.0	0.04	210.5	25.9
Elk02	48.9	601	1.05	2267	1.2	0.06	160.0	11.3
Elk03	51.4	679	0.43	2071	1.7	0.04	149.6	25.9
Elk05	52.7	441	1.19	2199	2.1	0.06	272.5	0.4
Elk14	51.1	360	0.83	2348	1.4	0.06	191.2	10.5
Elk27	51.6	780	1.13	2269	1.5	0.06	191.3	24.1
Deer4,12	55.3	152	0.70	2097	2.3	0.03	79.7	-3.3
Deer5,15	53.7	190	0.88	2116	1.7	0.04	65.6	2.5
Deer11,14	55.3	311	0.58	1763	3.8	0.03	117.8	2.5
2Bison01	56.1	1167	0.80	2033	2.8	0.06	296.9	42.2
2Bison03	55.7	1664	0.84	1897	2.8	0.05	282.8	50.0
2Bison06	58.3	1341	1.07	2114	2.2	0.06	274.4	33.2
2Bison08	57.3	1650	0.55	2131	3.8	0.04	317.7	56.2
2Bison45	55.1	1031	0.54	1986	3.6	0.03	282.2	30.0
2Elk02	54.4	1606	1.29	2368	2.6	0.07	420.7	41.6
2Elk03	55.4	1666	1.20	2431	2.6	0.07	427.2	40.5
2Elk05	52.2	1029	1.52	2326	1.5	0.08	239.2	37.2
2Elk14	51.2	1501	1.05	2108	2.8	0.05	324.0	42.5
2Elk27	53.9	1399	0.87	2196	2.4	0.06	297.0	38.6
2Deer1,2	56.1	300	1.11	2226	2.2	0.05	107.7	1.1
2Deer4,12	52.8	269	0.45	1866	5.2	0.03	149.0	1.2
2Deer5,15	55.7	401	1.06	2052	2.7	0.05	134.4	4.6
2Deer11,14	55.2	444	0.67	2009	3.8	0.03	130.4	7.9
Bison	**53.35**	**698.44**	**0.82**	**2109.08**	**2.89**	**0.04**	**224.32**	**11.91**
Elk	**51.14**	**572.29**	**0.93**	**2230.68**	**1.58**	**0.05**	**192.90**	**14.42**
Deer	**54.76**	**217.79**	**0.72**	**1992.00**	**2.60**	**0.04**	**87.69**	**0.56**
2Bison	**56.50**	**1370.61**	**0.76**	**2032.36**	**3.04**	**0.05**	**290.81**	**42.33**
2Elk	**53.40**	**1440.38**	**1.19**	**2285.93**	**2.38**	**0.06**	**341.60**	**40.10**
2Deer	**54.97**	**353.69**	**0.82**	**2038.18**	**3.48**	**0.04**	**130.38**	**3.71**

Feed Analysis for both digestibility and calorimetry trials

Animal	% DM	E kcal/kg	E kJ/kg	Protein %	Lignin %	% Ash	% NDF	% ADF
Bison01	95.39	4305	18012	13.76	10.93	8.28	59.38	43.52
Bison03	95.39	4305	18012	13.76	10.93	8.28	59.38	43.52
Bison06	95.39	4305	18012	13.76	10.93	8.28	59.38	43.52
Bison08	95.39	4305	18012	13.76	10.93	8.28	59.38	43.52
Bison45	95.39	4305	18012	13.76	10.93	8.28	59.38	43.52
Elk02	95.39	4305	18012	13.76	10.93	8.28	59.38	43.52
Elk03	95.39	4305	18012	13.76	10.93	8.28	59.38	43.52
Elk05	95.39	4305	18012	13.76	10.93	8.28	59.38	43.52
Elk14	95.39	4305	18012	13.76	10.93	8.28	59.38	43.52
Elk27	95.39	4305	18012	13.76	10.93	8.28	59.38	43.52
Deer4,12	95.39	4305	18012	13.76	10.93	8.28	59.38	43.52
Deer5,15	95.39	4305	18012	13.76	10.93	8.28	59.38	43.52
Deer11,14	95.39	4305	18012	13.76	10.93	8.28	59.38	43.52
2Bison01	95.00	4331	18120	14.09	11.18	8.34	58.99	43.40
2Bison03	95.00	4331	18120	14.09	11.18	8.34	58.99	43.40
2Bison06	95.00	4331	18120	14.09	11.18	8.34	58.99	43.40
2Bison08	95.00	4331	18120	14.09	11.18	8.34	58.99	43.40
2Bison45	95.00	4331	18120	14.09	11.18	8.34	58.99	43.40
2Elk02	95.00	4331	18120	14.09	11.18	8.34	58.99	43.40
2Elk03	95.00	4331	18120	14.09	11.18	8.34	58.99	43.40
2Elk05	95.00	4331	18120	14.09	11.18	8.34	58.99	43.40
2Elk14	95.00	4331	18120	14.09	11.18	8.34	58.99	43.40
2Elk27	95.00	4331	18120	14.09	11.18	8.34	58.99	43.40
2Deer1,2	95.00	4331	18120	14.09	11.18	8.34	58.99	43.40
2Deer4,12	95.00	4331	18120	14.09	11.18	8.34	58.99	43.40
2Deer5,15	95.00	4331	18120	14.09	11.18	8.34	58.99	43.40
2Deer11,14	95.00	4331	18120	14.09	11.18	8.34	58.99	43.40
Bison	**95.39**	**4305.00**	**18012.12**	**13.76**	**10.93**	**8.28**	**59.38**	**43.52**
Elk	**95.39**	**4305.00**	**18012.12**	**13.76**	**10.93**	**8.28**	**59.38**	**43.52**
Deer	**95.39**	**4305.00**	**18012.12**	**13.76**	**10.93**	**8.28**	**59.38**	**43.52**
2Bison	**95.00**	**4330.73**	**18119.79**	**14.09**	**11.18**	**8.34**	**58.99**	**43.40**
2Elk	**95.00**	**4330.73**	**18119.79**	**14.09**	**11.18**	**8.34**	**58.99**	**43.40**
2Deer	**95.00**	**4330.73**	**18119.79**	**14.09**	**11.18**	**8.34**	**58.99**	**43.40**

	% Digestibility's						
Animal	**DM**	**Energy**	**Nitrogen**	**OM**	**Lignin**	**NDF**	**ADF**
Bison01	50.89	52.09	55.81	53.65	0.79	43.99	42.33
Bison03	47.26	46.86	61.96	50.32	0.62	40.44	37.44
Bison06	40.11	46.49	42.08	48.36	-42.92	31.54	25.98
Bison08	61.09	60.79	69.54	62.44	20.31	52.98	50.08
Bison45	46.31	48.84	55.12	50.26	-4.84	36.92	32.92
Elk02	49.35	52.55	44.61	54.02	8.14	46.00	43.05
Elk03	51.57	51.02	55.27	54.20	17.97	45.36	42.80
Elk05	56.31	55.43	60.36	57.95	21.73	48.20	47.07
Elk14	57.40	57.54	60.85	59.73	24.41	50.95	50.03
Elk27	52.75	52.59	58.27	54.88	21.92	45.13	44.04
Deer4,12	38.12	35.50	47.51	40.40	-29.14	26.45	21.35
Deer5,15	51.50	50.11	61.82	52.90	-35.46	44.22	40.17
Deer11,14	47.02	46.85	58.19	49.07	7.81	37.63	32.72
2Bison01	54.16	56.36	63.13	57.37	14.98	42.13	40.75
2Bison03	45.68	45.96	59.31	48.58	1.83	34.25	30.26
2Bison06	45.66	49.27	59.55	51.88	-28.48	30.75	27.00
2Bison08	48.79	50.57	60.92	51.71	-7.05	38.18	32.42
2Bison45	49.00	52.60	59.71	54.22	-5.76	40.32	35.29
2Elk02	47.76	46.97	58.83	50.78	2.89	39.15	34.57
2Elk03	46.90	47.63	56.25	49.82	4.45	37.56	32.26
2Elk05	54.83	53.99	61.02	57.18	25.12	47.12	45.62
2Elk14	47.94	45.43	56.68	50.93	9.18	41.51	38.61
2Elk27	47.49	48.58	53.27	50.97	5.99	38.98	34.84
2Deer1,2	48.56	50.48	56.88	51.70	2.48	38.28	33.51
2Deer4,12	47.69	46.07	58.65	49.46	16.41	39.75	36.32
2Deer5,15	48.49	47.80	60.26	50.19	13.62	38.27	33.85
2Deer11,14	47.46	46.17	59.63	49.81	15.39	37.35	33.17
Bison	**49.13**	**51.01**	**56.90**	**53.01**	**-5.21**	**41.18**	**37.75**
Elk	**53.48**	**53.83**	**55.87**	**56.16**	**18.83**	**47.13**	**45.40**
Deer	**45.55**	**44.15**	**55.84**	**47.45**	**-18.93**	**36.10**	**31.41**
2Bison	**48.66**	**50.95**	**60.52**	**52.75**	**-4.89**	**37.13**	**33.14**
2Elk	**48.98**	**48.52**	**57.21**	**51.93**	**9.52**	**40.86**	**37.18**
2Deer	**48.05**	**47.63**	**58.86**	**50.29**	**11.97**	**38.41**	**34.21**

		Temperature °C———			Calorimetry———	
Animal	**Date(1995)**	**Max.**	**Min.**	**Mean**	**DMI (kg)**	**Dig. DMI(kg)**
Bison01	27-Mar	3.0	-13.5	-5.3	3.81	1.9
Bison03	13-Mar	12.0	-6.0	3.0	2.46	1.2
Bison06	10-Apr	2.0	-5.0	-1.5	3.35	1.3
Bison08	20-Mar	11.5	-3.0	4.3	4.28	2.6
Elk02	4-Apr	-5.0	-8.0	-6.5	2.87	1.4
Elk03	11-Apr	16.5	-3.5	6.5	3.73	1.9
Elk05	15-Mar	2.5	-1.0	0.8	2.52	1.4
Elk14	11-Apr	16.5	-3.5	6.5	2.70	1.6
Elk27	22-Mar	14.0	-3.0	5.5	2.98	1.6
Deer 1,2	28-Mar	2.0	-8.0	-3.0	1.89	0.9
Deer4,12	17-Mar	2.5	-8.0	-2.8	1.37	0.5
Deer5,15	24-Mar	2.0	-3.5	-0.8	1.98	1.1
Deer11,14	30-Mar	13.0	-7.0	3.0	2.06	1.0
2Bison01	22-May	15.0	1.0	8.0	4.35	2.4
2Bison03	8-May	20.0	-1.0	9.5	5.63	2.6
2Bison08	16-May	18.0	2.0	10.0	4.52	2.2
2Elk02	8-Jun	26.0	1.0	13.5	5.38	2.6
2Elk03	29-May	34.0	10.0	22.0	5.06	2.4
2Elk05	10-May	26.5	4.0	15.3	3.97	2.2
2Elk14	22-May	15.0	1.0	8.0	5.74	2.8
2Elk27	26-May	14.0	-3.0	5.5	5.31	2.5
2Deer1,2	27-May	22.0	5.0	13.5	2.88	1.4
2Deer4,12	15-May	23.5	1.5	12.5	1.65	0.8
2Deer5,15	18-May	21.0	5.0	13.0	3.11	1.5
2Deer11,14	1-Jun	32.0	10.0	21.0	2.70	1.3
Bison		**7.1**	**-6.9**	**0.1**	**3.5**	**1.8**
Elk		**8.9**	**-3.8**	**2.6**	**3.0**	**1.6**
Deer		**4.9**	**-6.6**	**-0.9**	**1.8**	**0.9**
2Bison		**17.7**	**0.7**	**9.2**	**4.8**	**2.4**
2Elk		**23.1**	**2.6**	**12.9**	**5.1**	**2.5**
2Deer		**24.6**	**5.4**	**15.0**	**2.6**	**1.2**

	CH_4 Production					
Animal	**L/d**	**g/d**	**kcal/d**	**kJ/d**	**L/kg DMI**	**L/kg dig DM**
Bison01	169.2	121.2	1607.6	6726.3	44.4	87.4
Bison03	101,5	72.7	964.6	4035.8	41.3	87.4
Bison06	87.7	62.8	833.0	3485.4	26.2	65.3
Bison08	184.6	132.2	1753.8	7337.7	43.1	70.6
Elk02	64.6	46.3	613.8	2568.2	22.5	45.7
Elk03	70.8	50.7	672.3	2812.8	19.0	36.8
Elk05	106.2	76.0	1008.4	4219.2	42.1	74.8
Elk14	66.2	47.4	628.4	2629.4	24.5	42.6
Elk27	110.8	79.3	1052.3	4402.6	37.2	70.5
Deer 1,2	43.1	30.9	409.5	1713.2	22.8	50.1
Deer4,12	24.1	17.3	229.3	959.4	17.6	46.2
Deer5,15	20.7	14.8	196.5	822.3	10.4	18.9
Deer11,14	25.9	18.5	245.7	1027.9	12.6	26.7
2Bison01	100.8	72.2	957.6	4006.4	23.2	42.7
2Bison03	118.1	84.5	1121.7	4693.2	21.0	45.9
2Bison08	148.3	106.2	1409.0	5895.1	32.8	67.2
2Elk02	104.4	74.7	991.5	4148.3	19.4	40.6
2Elk03	89.6	64.2	851.2	3561.3	17.7	37.8
2Elk05	77.8	55.7	738.7	3090.7	19.6	35.7
2Elk14	84.0	60.1	798.0	3338.7	14.6	30.5
2Elk27	98.0	70.2	931.0	3895.1	18.5	38.9
2Deer1,2	42.6	30.5	404.7	1693.2	14.8	30.5
2Deer4,12	25.6	18.3	242.8	1015.9	15.5	32.6
2Deer5,15	41.2	29.5	391.2	1636.7	13.2	27.3
2Deer11,14	35.5	25.4	337.2	1411.0	13.1	27.7
Bison	**135.8**	**97.2**	**1289.7**	**5396.3**	**38.8**	**77.7**
Elk	**83.7**	**59.9**	**795.0**	**3326.4**	**29.1**	**54.1**
Deer	**28.4**	**20.4**	**270.2**	**1130.7**	**15.9**	**35.5**
2Bison	**122.4**	**87.6**	**1162.7**	**4864.9**	**25.7**	**52.0**
2Elk	**90.7**	**65.0**	**862.0**	**3606.8**	**18.0**	**36.7**
2Deer	**36.2**	**25.9**	**344.0**	**1439.2**	**14.2**	**29.5**

		Metabolic Rate——
Animal	**CH_4 % of GE**	**HP kJ/kg$^{0.75}$**
Bison01	9.80	585.34
Bison03	9.11	419.81
Bison06	5.78	565.48
Bison08	9.52	688.71
Elk02	4.97	546.43
Elk03	4.19	727.94
Elk05	9.30	485.31
Elk14	5.40	618.60
Elk27	8.20	588.01
Deer 1,2	5.03	438.83
Deer4,12	3.89	428.23
Deer5,15	2.31	345.90
Deer11,14	2.77	1446.15
2Bison01	5.08	594.40
2Bison03	4.60	791.31
2Bison08	7.20	829.00
2Elk02	4.25	699.62
2Elk03	3.89	821.66
2Elk05	4.29	952.06
2Elk14	3.21	751.02
2Elk27	4.05	780.92
2Deer1,2	3.24	540.12
2Deer4,12	3.41	398.73
2Deer5,15	2.90	1647.90
2Deer11,14	2.88	1823.90
Bison	**8.6**	**564.8**
Elk	**6.4**	**593.3**
Deer	**3.5**	**664.8**
2Bison	**5.6**	**738.2**
2Elk	**3.9**	**801.1**
2Deer	**3.1**	**1102.7**

Energy of the diet					Intake		
Animal	GE kJ/kg	DE kJ/kg	ME kJ/kg	ME/DE	GE kJ/d	DE kJ/d	ME kJ/d
Bison01	18012.1	9382.7	5906.2	0.63	38582.0	20097.8	12651.0
Bison03	18012.1	8439.8	5849.6	0.69	33502.5	15698.0	10880.2
Bison06	18012.1	8374.1	6004.0	0.72	33466.5	15559.0	11155.5
Bison08	18012.1	10949.0	8330.7	0.76	60052.4	36504.1	27774.7
Bison45	18012.1	8796.4	.	.	69418.7	33901.2	.
Elk02	18012.1	9465.1	8130.5	0.86	43697.4	22962.3	19724.7
Elk03	18012.1	9189.0	7928.5	0.86	49137.1	25067.5	21628.9
Elk05	18012.1	9984.5	7184.4	0.72	34475.2	19110.3	13751.0
Elk14	18012.1	10364.5	8293.8	0.80	29828.1	17163.6	13734.5
Elk27	18012.1	9472.6	7847.6	0.83	57674.8	30331.1	25127.9
Deer4,12	18012.1	6393.6	4573.2	0.72	8015.4	5430.3	4620.2
Deer5,15	18012.1	9025.0	8011.7	0.89	13166.9	9882.1	9141.4
Deer11,14	18012.1	8438.9	7551.7	0.89	19110.9	14032.3	13090.9
2Bison01	18119.8	10211.8	9035.6	0.88	82227.6	46341.1	41003.5
2Bison03	18119.8	8328.5	7281.7	0.87	99622.6	45790.0	40035.0
2Bison06	18119.8	8928.4	.	.	76682.9	37785.0	.
2Bison08	18119.8	9163.8	7862.4	0.86	101941.9	51555.7	44234.0
2Bison45	18119.8	9530.4	.	.	66499.6	34976.4	.
2Elk02	18119.8	8511.3	7474.9	0.88	102485.5	48140.1	42277.8
2Elk03	18119.8	8630.1	7671.9	0.89	102666.7	48898.2	43469.1
2Elk05	18119.8	9783.3	8821.6	0.90	79038.5	42674.8	38480.0
2Elk14	18119.8	8231.6	7408.1	0.90	102086.9	46377.1	41737.1
2Elk27	18119.8	8802.1	7767.1	0.88	89656.7	43552.6	38431.6
2Deer1,2	18119.8	9146.0	7813.7	0.85	18826.5	14164.6	12780.3
2Deer4,12	18119.8	8346.9	7243.5	0.87	17648.7	12889.3	11814.5
2Deer5,15	18119.8	8661.1	7664.8	0.88	25331.5	18719.8	17327.0
2Deer11,14	18119.8	8365.1	7565.3	0.90	27759.5	20287.4	19062.1